# Short and medium range navigation and its relationship to cognitive mapping and associative learning.

by

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Submitted to the University of Edinburgh for the Degree of Doctor of Philosophy

July 1996

In accordance with the requirements of the University of Edinburgh regulation 3.4.7. this thesis has been composed by myself and the work presented herein is my own.

Robert Biegler

To my relief

**Acknowledgements**

The work described in this thesis was supported by a grant from the Wellcome Trust.

All the research described in this thesis was supervised by Dr. R. G. M. Morris, who taught me much about science in general, how to design and run experiments, not to start with the complicated bits when writing papers, and even managed to get through to me the importance of keeping good records of experimental procedures.

I thank Katalin Gothard for helpful, enjoyable and interesting discussions. Only because of the limitations of email they were less frequent and detailed than I would have liked. Mark Good taught me much of what I know about associative learning theory, but cannot be held responsible for my interpretations. Robert Steele, Joanna Bryson, Frances Fahy and Susan Dye commented on earlier drafts of this thesis. David Foster corrected the mistakes in my calculations in the appendix. Roger Spooner repeatedly modified software according to need. Finally, several scientific meetings stand out as especially informative and inspiring: The 1994 Nato ASI on Brain and Behaviour in Naturalistic and Semi-naturalistic Environments; the 1995 Navigation Symposium organised by the Company of Biologists; the 1996 symposium "Rules of Spatial Memory Organisation" at the Akademie der Wissenschaften, Berlin; and the 1996 European Neuroscience Programme School "Brain and Space". I thank the organisers and participants.

# Abstract

Learning allows organisms to predict and prepare for events in the environment that are not sufficiently regular that responses to each situation could be genetically hardwired. A possible categorization of what can be learned is as follows: First, an animal may learn that an event is likely to happen. This means learning predictive relations between events, or the probability that an event A occurs with an event B, rather than independently. Second, they may form a representation of the magnitude of the event. Third, animals may learn when an event is likely to happen, the temporal relations between events. Fourth, they may acquire knowledge where something will happen, the spatial relations between events.

The question arises whether these distinctions are merely convenient labels or reflect genuine differences between dissociable psychological variables and perhaps processes. The most widely accepted account of animal learning, associative learning theory, assumes that information from all these variables is collapsed into only a single output variable: the strength of an associative link. The theoretical framework of associative learning has predominantly been developed and tested within the domain of learning about predictive relationships between events, weighted by event relevance. The requirements for navigation through space are in some respects quite different. Animals can influence the rate and direction of their passage through space. In the two or three dimensions of space shortcuts and detours become possible. The computation of path length may require vector addition.

Possible goals of computation will be considered and compared to data on the contents, acquisition and manipulation of spatial representations. The experimental part of this thesis concentrates on two aspects of information acquisition, landmark stability and blocking. Animals appear to weigh information from different sources according to two different and normally opposed criteria, accuracy and reliability. If discrepancy between two such sources is small, more weight will be given to the more accurate source of information, if the discrepancy is large more to the reliable source. The experiments on landmark stability suggest that manipulating discrepancy throughout training will influence animals' estimate of reliability of a source of information. Other manipulations of this estimate, independent from discrepancy, are also possible. The experiments on blocking have not yielded a simple result. Blocking occurs when the animals were trained with one of two landmark arrays; the other array led to an enhancement of performance when testing

with the added landmarks. In addition, previous work on the "geometric module" has been extended and a novel weighting of landmarks by position in the array, rather than distance from a goal, has been found.

It is argued that ~~there~~ associative learning can play a role in the creation of most possible representations of space, but that some aspects of navigation involve computations which associative learning is not capable of. Further, consideration of the possible functions of navigation suggests that there is no clear dichotomy between mapping and non-mapping strategies. The features of cognitive maps derived from analogy with physical maps do not form an indivisible category. A navigational system may have only some of these properties, depending on what is required of it. The supposed incompatibility of cognitive mapping and associative learning does not exist, both because there are several navigational strategies that could be considered cognitive mapping processes and because associative learning could contribute to most of them.

# Contents

A party of pschologists goes hiking in the mountains. After a few hours they are completely lost. One of them takes the map and compass, takes the bearings of distant landmarks, checks the position of the sun, and so on. After a while he says:

"Do you see that big mountain over there?"

"Yes?"

"Well, according to the map we're right on top of it."

# Introduction

Learning allows organisms to predict and prepare for events in the environment that are not sufficiently regular that responses to each situation could be genetically hardwired. A possible categorization of what can be learned is as follows: First, an animal may learn *that* an event is likely to happen. This means learning the predictive relations between events, or the probability that an event A occurs with an event B, rather than independently. Recognition and categorisation may be included here as it requires learning which features occur together in any particular situation. Second, animals may form a representation of the *magnitude* of the event. This could be the size of a food item, the rate of energy intake in a foraging patch or perhaps the degree of injury and pain incurred from fighting a dominant competitor or a predator. Third, animals may learn *when* an event is likely to happen, the temporal relations between events. Fourth, they may acquire knowledge *where* something will happen, the spatial relations between events. Knowledge about the reliability of estimates of magnitude, temporal and spatial relations would raise the possible number of variables to be represented from four to seven. Magnitude might even be subdivided further into components of size and number, or intensity and duration, raising the number of variables still more.

The question arises whether these distinctions are merely convenient labels or reflect genuine differences between dissociable psychological variables and perhaps processes. The most widely accepted account of animal learning, associative learning theory, assumes that information from all these variables is collapsed onto only a single output variable: the strength of an associative link. The theoretical framework of associative learning has predominantly been tested and developed within the domain of learning about predictive relations. Within this domain some phenomena once considered a challenge have been absorbed into associative learning theory: for example biological constraints in the form of associative predispositions, which may be species-specific; or long delay learning, found most frequently, but not exclusively, in taste aversion learning.

Another challenge to the general applicability of associative learning theory comes from the study of animal navigation, which has computational requirements that appear to be quite different. Animals can influence the rate and direction of their passage through space, in the two or three dimensions of space shortcuts and detours become possible and the computation of path length may require vector addition.

The navigational competence of animals and its relationship with theories of associative learning and cognitive mapping is the focus of this dissertation. To that purpose I will attempt a characterisation and classification of spatial representations and computations as well as examining how associative learning and/or cognitive mapping can be applied to these problems. This will require some discussion of the characteristics and constraints of both types of theories and how they relate to each other.

A key argument is that some of the confusion surrounding the question whether there are cognitive maps is due to there being numerous kinds of possible navigational strategies, with varying degrees of sophistication and flexibility. Some of these can be used in parallel and largely independently. Some may be integrated into a single system. Two to five of these possible navigational systems could be called cognitive mapping systems, depending on one's criteria. Likewise, discussion of the applicability of associative learning suffers from an assumption that there is only one, possibly two, navigational systems, all primarily landmark driven. I hope to show that in most possible systems (that I was able to find) associative learning could play a role, but that in only very few of these systems it could deal with all necessary storage of information in memory.

Chapter 1 examines representations of the environment at a conceptual level. What are the possible functions of representations? What kind of information might be useful in a representation? Would there be one system storing and processing that information or several? What are the relevant levels of analysis?

Chapter 2 elaborates on some of the points raised in section 1.5, the goals and computational requirements of navigation, by examining navigational strategies using information from either external landmarks or from 'path integration' or 'dead reckoning'. In both cases several strategies of varying flexibility are possible. Some relevant behavioural evidence is discussed, but due to the sheer volume of that literature (and my limited familiarity with some of it) this review must necessarily be selective.

The topic of chapter 3 is the integration of spatial information. I will argue that dead reckoning and landmark information complement each other. Depending on the level of sophistication of each strategy, the combination may be sufficient to provide most of the capacities postulated for cognitive maps, even when neither component on its own would be sufficient.

After these considerations of the contents and structure of spatial representations,

chapter 4 will turn to the conditions of information acquisition, in connection with my own experimental work on landmark stability. To keep this thesis reasonably concise only those experiments will be reported that provided interesting results. The numerous pilot studies will be ignored.

Chapter 5 will deal with another aspect of the conditions of learning, blocking and overshadowing, and an experiment examining blocking in the spatial domain.

Chapter 6 contains the summary and conclusions. I will argue that contrary to the claims of advocates of either cognitive mapping or associative learning, these two theoretical approaches are not incompatible. This very much reduces the importance of the question whether associative learning can account for navigation. There are many possible navigational strategies, and the answer depends on what strategy is being used in any particular situation. Likewise I suggest that there are several possible systems that could be said to perform cognitive mapping. There is experimental evidence for some of them, but not others. Questions about cognitive mapping or associative learning in navigation are answerable, if care is taken in the formulation of the question. The polarisation of this issue into a mutually exclusive distinction between cognitive mapping and associative learning is misleading because several issues are confounded.

# 1. Representations of the environment

This chapter examines the functions of representations, the operations performed on them, and the implications of various assumptions implicit in theories of learning. A fundamental constraint of associative learning theory is its insistence on a single output variable, the associative strength. An alternative class of theories assumes that primitive variables are stored and can be combined to produce derived representations. This offers, in principle, greater flexibility, one of the proposed characteristic features of cognitive maps. It also raises the question whether there are specialised and distinguishable learning and memory systems. If so, what makes a division into several systems necessary and what could be done within a single system?

## 1.1. Some thoughts on the nature of representations

The function of representations is to manipulate and combine information in such a way that other information can be derived that is not directly available. This is not necessarily a high-level 'inferential' or 'cognitive' process. For example, sound is inherently directional. The ears of fishes have directionally sensitive hair cells arranged in ordered fields. Information about the direction of a sound source is available at the level of the sensory epithelium. Impedance matching between air and the fluid surrounding the hair cells, and the required channelling and concentration of sound energy, makes this impossible for terrestrial animals. They must derive sound direction from intensity and phase differences between ears. The barn owl uses this information to compute azimuth and elevation of sound in head-centered coordinates and combines them in a two-dimensional map where direction is represented as a patch of neural activity (Knudsen et al., 1987). On a slightly more abstract level, a hummingbird could use a representation of the location and appearance of a patch of flowers, together with the time since they were last emptied and the rate of replenishment, to determine whether and when it is worth to visit this patch again, without having any current sensory information about the state of this patch.

To fulfil such a function there must be some correspondence or isomorphism between the representation and the environment. An isomorphism exists when the mapping between entities in the represented and the representing system preserves relations and operations, so that there is a relation between entities in the representing system if and only if there is a corresponding relation between entities in the

represented system (see Gallistel, 1990, for an extensive review). The reverse need not be true, and in psychology is unlikely to be true, as the representing system may not contain all properties of the represented system. The relations in the representing system also may only approximate the relations in the represented environment, and that possibly only over a restricted range that is particularly relevant.

Whether different computations are necessary to deal with different types of information depends on the nature of the representations employed and the richness of the isomorphism between the represented and the representing system. A neuron responding to a feature is sometimes said to represent that feature. If the mapping between represented and representing system preserves only presence or absence of the feature the isomorphism is restricted to identity. This is the most impoverished form of representation and it does not require any specialised computations. An example of a richer isomorphism is mental rotation. The time required by human subjects to match a sample stimulus to a rotated comparison stimulus increases linearly with the degree of rotation (Shepard and Metzler, 1971). The inference is that a representation of one of the stimuli is rotated and compared with the other. This operation is equivalent to an operation that could be performed on a physical object and presumably the computational requirements are different from those for, say, timing a response.

## 1.2. Some relevant features of associative learning theory

Learning about predictive relations has been studied extensively and successfully within the framework of associative learning theory. In this review, associative learning theory is defined as the assumption that learning can be adequately described by specifying the strengths of associations between stimuli (or their features) and the rules governing the change of associative strength (Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972; Sutton and Barto, 1981, 1989; Wagner, 1981)

The asymptotic strength of an associative link is assumed to be proportional to some aspect of the significance of the predicted event, such as average rate of food delivery or strength of a foot shock. However, associative strength does not directly represent the importance or size of the signalled event. It also depends on the predictive relationship between conditioned stimulus (CS) and unconditioned stimulus (US). It can be considered a compound representation of relevance: a combination of the importance of the US and of the strength of the evidence for its

imminent occurrence that is provided by the CS. Put another way, associative learning detects statistical invariances and weights them by their relevance to the animal. Rescorla (1968) found that the associative strength of a target depends on its correlation with the US. i.e. how well it predicts the US. Wagner et al. (1968) discovered that the associative strength of a target stimulus is also influenced by "relative validity", how well other stimuli predict the US. When given a range of stimuli that signal an interesting event, animals will concentrate on the best predictor, to the detriment of other stimuli.

Additivity is largely preserved within this compound representation of relevance. If two stimuli predicting the same consequence are separately conditioned to asymptote and then presented simultaneously the subject will expect a US of larger magnitude, a phenomenon known as overexpectancy (Kremer, 1978; Rescorla, 1970). If the magnitude of the US does not change, the associative strength of both stimuli will decrease. Alternatively, if a third stimulus is added it will become an inhibitor. Inhibitory stimuli predict the absence or reduced magnitude of an otherwise expected US. When combined with an excitatory stimulus of equal strength the overall prediction will be the same as in absence of all stimuli. However, additivity is not always strictly preserved. If a stimulus A has been trained to asymptote, and then stimulus B is added and the US is omitted, B will become an inhibitor. If the magnitude of the US is reduced, the strength of the inhibition should depend directly on the reduction in magnitude of the US. If the US remains the same, inhibition, as well as excitation, are zero. This is a blocking procedure. Instead it has been found that reductions of US magnitude can lead to unblocking (Dickinson et al., 1976; Dickinson and Mackintosh, 1979; Mackintosh and Cotton, 1980) rather than inhibitory conditioning. This is one of the failures of the Rescorla-Wagner (1972) model, whose central assumption is one of strict preservation of additivity.

If a CS is presented either in isolation or uncorrelated with the US subsequent conditioning of this stimulus to the US will be retarded. Conditioning to a US of magnitude A will also retard subsequent conditioning to the same type of US of a larger magnitude B (Pearce and Hall, 1982). This phenomenon of latent inhibition is usually described as due to a decrease of a learning rate parameter. A low setting of the learning rate could be taken to represent a high degree of confidence that the associative strength is set at the correct value. However, the learning rate only influences the rate of change in associative strength, which remains the only output of the learning process. The learning rate parameter is not directly accessible. By its

nature it also would not allow an animal to distinguish between a highly variable rate of occurrence and a transition from one rate to another, both with low variance.

The function of associative processes has sometimes been characterised as "*detecting and storing information about the causal texture and structure of its environment*" (Dickinson, 1980; p. 8). It is important to distinguish between understanding the relationship between cause and effect and merely being able to predict events. As Dickinson himself points out, "animals may not possess the necessary sensory mechanisms to detect the actual proximate cause of a particular event" (p.8). Just as importantly, it may not have the cognitive capacity to identify a cause even if it does have the necessary sensory apparatus. This point is illustrated by the studies of Visalberghi and coworkers (Visalberghi and De Lillo, 1995; Limongelli et al., 1995; Visalberghi et al., 1995) using the trap tube task. A reward is put into a transparent plexiglass tube. The subjects, monkeys or apes, are provided with various sorts of stick, some immediately useful for pushing the reward out of the tube, some only after modification. The tube may be replaced by one with a trap in the centre. If the reward is pushed in the wrong direction, it will fall into the trap and cannot be retrieved. Variations on this task showed that at least some of the apes did show understanding of causal relationships. In contrast, capuchin monkeys (Cebus apella) did not understand what made a particular tool or procedure successful. If the trap was located off-centre, monkeys would still push the reward away from the centre, even if that pushed the reward into the tube. If the tube was turned so the trap pointed up, and the reward could not fall into it, monkeys still carefully selected the direction in which to push the reward, even though that made no difference any longer. They seemed to rely on associative rules, push away from the centre or away from the trap, that failed when the task was modified. There is no known difference in sensory capacities that could account for the difference. Rather than representing causal relations, associative learning appears to be a specialised mechanism for detecting correlations, weighted by their significance to the animal.

Associations may form hierarchies. Rescorla (1991) has reviewed evidence that animals can not only form binary associations between a stimulus and a response (S-R) a response and an outcome (R-O) and a stimulus and an outcome (S-O, more often referred to as S-S association for Stimulus-Stimulus), but that there can also be associations between a stimulus and a response-outcome complex (S-(R-O)). Of those associations only the S-O, R-O and S-(R-O) associations can be considered to represent a predictive relation. An S-R association is a consequence of responding to

a previous predictive relation, an autonomous habit not requiring further processing. Holman and Mackintosh (1981) have presented evidence that discriminative stimuli, $S_D$, which predict a contingency or R-O correlation, and conditioned stimuli, CS, form independent associations. An $S_D$ can block learning about another $S_D$, a CS can block another CS, but an $S_D$ cannot block a CS and a CS cannot block an $S_D$. Despite the evidence for separate associations, the account given by associative learning theory is restricted to a compound prediction of the fact *that* an event is likely to happen and of its magnitude, where an event may be a stimulus, the consequence of a response or a contingency. Time and space can only be accommodated as attributes of an event, no different from any other feature. Variability can only be represented by discounting or nonlinear weighting of events. This necessarily confounds the mean of a variable with its statistical uncertainty. Where several events contribute to the formation of an association, the associative link also cannot keep a record of the individual events. Different event histories leading to the same associative strength are indistinguishable (independence of paths). If during learning some form of discounting occurred, and changing conditions make a different discounting criterion more appropriate, then the association cannot be adjusted without further experience. The necessary information has been lost.

## 1.3. An alternative approach

Gallistel (1990) disputes that associations are the primitive building blocks of learning even within the domain of predictive relations and/or event magnitudes. They can only offer compound representations of several variables, in the examples discussed so far magnitude (for simplicity rate of occurrence has been lumped with this), probability and statistical uncertainty. Gallistel argues that phenomena such as overshadowing, blocking, latent inhibition and others, conventionally explained as a consequence of competition for a limited total sum of associative strength or associability, are in fact emergent features of the interactions between more primitive variables. Rate is assumed to be computed from the number and size of individual events, and the temporal intervals between them. Temporal intervals themselves are said to be secondary representations, calculated from differences in time of occurrence. In Gallistel's theory of learning, the variables contributing to an animal's choice of action are explicitly and separately represented, and their isomorphism with the corresponding aspects of the environment is rich. Numbers can be multiplied by sizes; times and numbers can be added and subtracted. The product of number and size can be divided by a temporal interval to yield rate. It is this richness of

isomorphism and the versatility of computations that can be performed with these representations of primitive variables that lead Gallistel to call this the computational-representational approach.

Gallistel considers associative learning to be a non-representational or subsymbolic theory, on the grounds that it must compound several of what he considers primitive variables in a single computation. In so far as Gallistel's postulated computations accurately describe behaviour, the single computation of an associative strength must effectively combine the properties of all these separate computations. If all computation took place in informationally encapsulated modules and if only the final combined output were accessible to determine behavioural output, Gallistel's theory and a suitable associative learning mechanism computing the same function would be indistinguishable by behavioural testing. A distinction would be possible only if the output of each of the computations Gallistel postulates were to be individually accessible and could be passed on to other processing if necessary. The representational approach would then allow increased flexibility. However, it is not clear that associative mechanisms can perform all the computations postulated by Gallistel. He argues they cannot. On the other hand it is not clear whether Gallistel's characterisation of the computations performed by animals is the most appropriate.

## 1.4. Levels of analysis

Gallistel believes that a computational-representational approach provides strong constraints in the design of models of cognition. He argues that for every problem there will be few, often only one adequate computational model. At first sight, this appears to be in sharp contrast to Anderson (1990) who claims that for every computation it is possible to develop an infinite number of mechanistic models, many of them indistinguishable by their output and even the time course of computations. The difference lies mostly in the level of analysis.

Anderson suggests four levels of analysis. The most abstract is the rational or adaptive level, similar to Marr's (1982) computational level and related to optimality theory. It is basically a characterisation of the problems posed by the environment. It specifies the goals of computation. Under the additional assumption that often there will be only a single best solution to a problem and that cognition adopts that solution, it constrains possible solutions. The level of algorithm specifies the actual computation performed. The level of implementation concerns itself with details such as how many memory stores there are and what their capacity is, whether

processing is parallel or serial, etc. The biological level deals with the operation of neurons. Anderson makes two important points about these levels of analysis. First, that ultimately only the algorithm level and and the biological level are directly relevant to what happens in a brain. The rational level only provides the demands posed by the environment. The level of implementation is only an approximation to the biological one. It is necessary both because usually not enough is known about the biological level, and to simplify analysis. Nevertheless, evolution only selects computations to be performed, which are realised only on the biological level.

Second, that there is a problem of identifiability at the implementational level. Work on formal machine theory has shown that there is an infinite number of mechanisms that compute the same input-output function. The problem gets worse the more complex the function is, as there are more possible ways of computing it. Physiological data can help constrain choices, but need to be detailed to avoid using the wrong constraints. Anderson remarks that three very different theories of cognition have all been proposed and defended in terms of neural timing.

Occam's Razor and its incarnation as Morgan's Canon, that one should assume that any given behaviour is controlled by the simplest possible mental process, may provide a useful heuristic for choosing between hypotheses. Nevertheless, there are several problems with this principle of parsimony. It is often possible to rank different mechanisms of the same type according to their complexity, but it would be hard to compare different types of mechanism, for example a production system and a neural network. Mittelstaedt (1961) pointed out that the same behaviour might be generated by simple interactions between complex elements or complex interactions between simple elements. Which system would be more parsimonious? A quantifiable measure of simplicity and complexity would need to be applied, a notoriously difficult problem (Cohen and Stewart, 1994). It is also necessary to assume that evolution chose the most parsimonious solution, which is demonstrably not universally true. For example, Heiligenberg (1989, p. 273) summarises research on processing of electrosensory information in electric fish as follows: "The analysis of brain mechanisms commonly reveals designs that human engineers would not have chosen. Brains appear to be built rather sloppily and are full of imperfections and patchwork which has accumulated in the course of their evolution" (for more details see Heiligenberg 1987).

Parsimony does not appear to be a good criterion for choosing hypotheses on the biological and implementational levels. Is it applicable at the level of algorithm? A

parsimony heuristic has some of the limitations of an optimality analysis. Evolution can only reach local optima, and there may be no evolutionary path to the most parsimonious solution of a problem. It is also not clear why there should be evolutionary pressure for parsimony as such. Simpler systems might be less error prone, but then resistance to errors would be the trait selected for, rather than parsimony itself. Further, what is parsimonious may depend on the assumptions made about the function of a process. What appears unnecessarily complex for a small task domain may be barely adequate if this process is a solution to a larger domain of problems. Of course, the reverse applies as well. I suggest that the principle of parsimony is a useful guide at Anderson's rational or adaptive level of analysis. When determining what a behaviour is for, one should make the simplest possible assumption. Parsimony is not applicable at the level of algorithm and implementation, which is the level at which the distinction between associative and other forms of learning is made.

Returning to the adaptive level and analysis of optimal solutions, Anderson points out that the most difficult part of this approach is an adequate characterisation of what a system's function is. This is illustrated by Gallistel's (1990) approach to navigation. He assumes the purpose of animal navigation is to answer the question 'where is X?' with X being either locations of interest to the animal, or the animal itself in relation to relevant locations. These two are equivalent. This question leads him to assume that effectively all animal navigation is based on metric maps of the environment. I will argue that there are other questions one could ask of a navigational system, defining a smaller task domain and requiring only systems simpler than metric maps.

## 1.5. Computational goals of and requirements for navigation

In the most general terms, the goal of navigation is to have the capacity to reach a specific location different from the current one. In other words, the question is not 'where is X?', but 'how can I reach X?' This destination X could be food, water or another resource, or cover from predators. Animals that have a home need a way to return to it. The most basic requirement for this is to recognise a goal location once it has been reached. In the absence of any other information, a goal could only be reached through a random walk. In a two or three dimensional search space this is clearly too inefficient to be useful. A method of finding a reasonably efficient path to a location is required. Recognition of a location once there will be taken for granted from here on.

The simplest possible way of returning to a place is to lay down a trail when leaving and to retrace it later. Limpets can follow their own slime trails to return to the spot on the rock where the shell exactly fits the surface and will provide a secure seal (Cook et al., 1969; Blackford-Cook, 1969). Other molluscs use the same strategy (Cook, 1977). Ants lay odour trails to recruit other foragers (Wilson, 1971). This strategy does not require representation of spatial relations in any form. It is computationally simple, but has several problems. If there are localised resources and trails cross at a home location, the organism would have to mark return trails from each resource differently in order to be able to choose between them. Revisiting a resource it must retrace a possibly quite tortuous outward path. The trail may fade with time. Until it does it could be followed by competitors or predators (Gehlbach et al., 1971; Gonor, 1967; Paine, 1963; Webb and Shine, 1992) which may either use and deplete the resource or eat the animal that laid the trail.

These problems suggest additional properties which would make a navigational system more useful. It should be able to identify and find one among several possible destinations. The path there should be reasonably efficient. Relevant information should only be identifiable as such in memory, rather than recognisable by other organisms. Information may be either internal (efference copies, vestibular and kinesthetic cues) or external (visual, olfactory, auditory, magnetic, etc.). It may be used either to find a direction that takes the animal closer to the goal, or to compute the spatial relationship between agent and goal. Several strategies are possible.

If a destination has a conspicuous feature perceptible at a distance, the animal only needs to recognise and approach this beacon. As the appearance of a visual beacon may depend on the direction of approach, and as more details become perceptible during approach, recognition under all those conditions can be a complex problem. The navigational aspect is fairly simple. Sounds or chemical gradients may also serve as beacons. Following an extended cue, for example a river's edge, is a special case of beacon navigation. These methods of navigation have also been called 'guidance strategies' by O'Keefe and Nadel (1978). Direct approach of a perceptible beacon assures an efficient path. If a beacon is too far, chaining could still make it possible to reach the goal, but it is not certain how efficient the path would be. Identification of beacons allows choice between different destinations.

If there is no beacon, the next option is to store a "snapshot" or "local view" of the environment as seen from the goal. (As use of these terms is quite inconsistent, it must be made clear that in this manuscript they refer to image-like representations

without information about distances of objects or the spatial relations between them, other than their sizes and their separation on the image.) There are three ways of using a snapshot for navigation. The animal may proceed by a chain of stimulus-response associations from snapshot to snapshot until it reaches the goal. The response may be any combination of turning through an egocentrically defined angle, turning towards a cue or in a compass direction; and to travel for a specific distance or until hitting the next familiar place. In these cases the snapshots are used only for place recognition. Alternatively, the animal moves so that a measure of mismatch between remembered snapshot and currently perceived scene decreases. Or else there must be an algorithm that computes from the mismatch a direction that takes the animal closer to the goal (Cartwright and Collett, 1983, 1987). This method effectively creates a virtual beacon where there is none in reality. None of these methods requires representation of spatial relations.

Information about metric spatial relations is needed to compute the costs of travelling between, for example, patchily distributed resources. The time and energy needed depend on distance and possibly terrain. Metric information is also necessary to plan and execute a trajectory in the absence of continuous feedback. One way to represent metric relations is through a list of landmark-goal and possibly landmark-landmark vectors. The creation of a vector list requires the correct assignment of distances and angles to the corresponding landmarks. Angles can only be defined by reference to three points or two points and a direction. A vector list is not necessarily internally consistent. Adding up two different series of vectors to the same destination could give two different resultant vectors. If vectors AB and BA are listed separately, there is not even a guarantee that AB is equal to the reverse of BA.

Finally, a map might be defined as an internally consistent representation where information about all relevant aspects of the environment is integrated. It might also be characterised as using only implicit representation of spatial relation, reducing redundancy of stored information. This rather vague definition will be elaborated later in relation to specific theories and models.

Internally generated information is, in the simplest case, only used to integrate velocity and direction into distance from home, and memory of distance travelled is reset to zero only at the home location. This is called dead reckoning or path integration. It would not seem entirely appropriate to call something a representation of space that contains information about only two points, home and the animal's current position, the latter not even fixed. Retaining information about locations

other than home becomes possible if path integration is initiated at these locations or if the vector to home can be stored and reversed. Multiple journeys to points other than home make it necessary to have an external directional reference at least at the home location to prevent accumulation of directional errors while at home or on other excursions. Return only to home may be possible by exclusive reference to internally generated directional information because the time span of integration is shorter. Internally generated information must necessarily be metric in order to be of any use because it cannot by itself provide any feedback. It may be reset at specific well known locations.

## 1.6. Associative learning in navigation

Given the restriction to a single output variable, the simplest associative accounts of navigational competence involve trail following, beacon navigation or the association of a snapshot with either a response or reward. If a snapshot is associated with a response, the animal would follow chains of stimulus response associations that cover the area an animal has previously traversed (Deutsch, 1960). The view of the environment available at each location would trigger the response that takes the animal to the next remembered location. This procedure would be relatively inflexible and construction of an optimised route fairly slow. Alternatively, the animal could move so as to reduce the discrepancy between a remembered and the currently perceived scene. This requires at least a measure of discrepancy or the sign of change, or better, an algorithm that provides the correct direction of movement (see Cartwright and Collett, 1983, 1987). Multiple snapshots might be used to construct a route longer than the range of any individual snapshot, or distal landmarks might be used for long range navigation and proximal landmarks close to the goal.

Regardless of whether they are associated with response or reward, snapshots may also be classified as one of two types. Either animals can disregard irrelevant features in the same way as bees differentially weight nearby and far landmarks, even when retinal size is equated (Cheng et al. 1987). Then contingency would affect landmarks in the same way as any other stimulus in conventional conditioning tasks. Rescorla (1968) found that the associative strength of a target stimulus depends on its correlation with reward. Wagner et al. (1968) discovered that it also depends on the relative validity of other, competing stimuli. Other commonly found phenomena are overshadowing, blocking (Kamin, 1969), latent inhibition (Baker and Mackintosh, 1979; Lubow and Moore, 1959) and overexpectancy (Kremer, 1978; Rescorla, 1970). The strengths of snapshot-reward associations should react to such manipulations in

the same way.

Alternatively, all visible features of a scene could be included in the snapshot, entering into a configural association (Sutherland and Rudy, 1989). The manipulation of contingency necessarily introduces variability between exposures to an environment. If a configural association must include all features, then this variability will force an animal to create as many configural representations as there are combinations of features. In the absence of generalisation, each combination would be unaffected by learning of other combinations and there would be no contingency effects.

Snapshot models appear to be the default assumption when associative learning is applied to the spatial domain, but more complex interpretations of associative learning theory are possible. I hope to show that there is no clear dividing line between these and some cognitive mapping models. Discussion of this grey area will be delayed until after a consideration of cognitive mapping.

## 1.7. Cognitive mapping

The minimal requirements to call a spatial representation a cognitive map are that it should have internal consistency and give the ability to plan routes in advance, including novel detours and shortcuts. The most influential definition of cognitive mapping, by O'Keefe and Nadel (1978) went considerably farther. O'Keefe and Nadel derived the properties of cognitive maps by analogy with physical maps and by contrasting them with routes. Routes are said to contain little information, already sequentially organised. Therefore they are assumed to be fast and easy to use, to require no special strategies for encoding spatial information and they may not be easily reversible. Maps contain a great deal of information without redundancy, are relatively invulnerable to loss of information and more flexible. Their use requires knowledge of the strategies used to encode spatial information, which takes more time than reading out a route. As is normal in a physical map, the presence of an object at any particular location can only be encoded in an all-or-none fashion. Mismatches between map and environment are rectified whenever detected. Mapping requires a stable environment. If a particular object keeps generating mismatches by moving its location frequently, it must be excluded from the map. If mismatches are frequent in a specific area, it has no stable structure that could be mapped. "*Whenever an organism attends to an object it is encoded in the map. ...the locale system will work in such a way as to direct the animal's attention away from objects it can predict towards those whose presence was unexpected. ...*

*Incorporation of information about stimuli occurs in non-incremental fashion. ...variability makes it difficult, if not impossible, to build a useful map*" (O'Keefe and Nadel, 1978, p. 95). A further implication is that there should be no overshadowing or blocking within the cognitive mapping system. The theory even permits the prediction that learning about new cues could be facilitated as it would only be necessary to make a new entry into an existing map.

Are there any other reasons for postulating a difference between spatial and other learning? A fundamental issue is whether spatial learning differs qualitatively from associative learning by virtue of certain unique features of space that do not apply to the correlational/temporal domain in which the vast majority of studies of associative conditioning have so far been conducted. For example, in a one-dimensional domain there are no shortcuts or detours, which would require vector addition to compute their lengths. Similarly, animals can influence the rate and direction of their passage through space, but not through time. The use of cognitive mapping is a frequently suggested solution to these problems (Gallistel 1990; Gould, 1986; O'Keefe and Nadel, 1978), but is contentious (Bennett, 1996; Dyer, 1991; Wehner and Menzel, 1990).

It may be best to examine the necessary features of a map by comparison with representations that are simpler than maps, yet are more complex than the snapshot models described above. A map should be internally consistent. A representation consisting of lists of landmark-goal vectors (Cartwright and Collett, 1986) would not necessarily fulfil this condition. Assume an animal is travelling by one of two routes from point A to point B. It has lists of vectors giving distances and directions between points on these routes. Vector addition of the components of the two routes may give two different overall distances and directions. If the errors along each component are sufficiently small, this would not affect the usefulness of the representation. Planning routes in advance requires an integrated representation of metric parameters. Assume an animal has seen its destination, but must detour around an obstacle and through an area that only allows another view of the goal at a very short distance. This would be a common problem for a predator whose goal is prey and the obstacle an area of insufficient cover. Determining the correct direction and distance once the detour is completed requires knowledge of both distance and direction of the goal at the point where it was last seen, and knowledge of the path travelled since then. A snapshot algorithm cannot provide the first. The second requires the ability to start path integration at any arbitrary point, then add that

displacement vector to the last perceived goal vector. If an animal loses its way and manages to find a familiar landmark, then in the absence of further landmarks it would need to reset path integration to its current location. This is not an ability to be taken for granted. Wehner (1996) found that once desert ants had reeled off the return vector to the nest, from a feeding station surrounded by conspicuous landmarks, they were unable to duplicate this same route when caught at the nest and returned to the same feeding station.

## 1.8. Intermediate models

Both the standard associative models and O'Keefe and Nadel's cognitive map model propose links between the contents and the conditions of learning (see Dickinson, 1980, pp. 22-25). The associative models start with the study of the conditions of learning, draw inferences about mechanisms (associative links) and postulate representations and computations that best fit this mechanism. O'Keefe and Nadel derived the putative properties of cognitive maps from analogy with physical maps, and inferred from this representation likely computations and conditions of learning. The proposed links between contents and conditions seem plausible, but are not necessary. It is at least conceivable that contents and conditions are largely independent parameters. Animals might use spatial representations richer than a snapshot, possibly even maps, but that information could be added according to the rules of associative learning. Blocking and overshadowing might occur because adding information to the map entails a cost, for example time spent exploring rather than foraging. Then not all available information would be incorporated, only as much as is necessary at the time. As an example, a model recently described by McNaughton et al. (1996) could bridge the gap between the two approaches. It is suggested that hippocampal place cells encode location within distinct multiple reference frames rather than a unitary global map (see also Gothard et al., 1996). The representation of locations within a reference frame is preconfigured to be internally consistent even in the absence of experience. The primary means of navigation is assumed to be dead reckoning and landmark information gets added only secondarily. This is assumed to be an associative process, while the structure of reference frames would give map-like properties to the representation of space. Sutherland and Rudy's (1989) configural association theory might also create a map-like representation if spatial properties are assumed to be part of configural associations. In both cases the specification of a location relative to landmarks would be a step separate from associating that place with reward or response. In neither case is the type of

landmark information yet defined in sufficient detail to make testable predictions concerning its acquisition and use. The complementary suggestion, the representation of space by associative links that are established according to rules different from those found in conditioning, has not, to my knowledge, been put forward in a coherent theory, though some models do use competitive learning for restricted aspects of a task (see section 2.5).

## 1.9. Are there parallel systems?

The dispute over the nature of spatial learning is part of a greater disagreement over whether there is a generalised learning mechanism or whether evolution has provided a lot of specialised and possibly independent mechanisms, each adapted to an aspect of its owner's ecological niche (Revusky, 1977; Rozin and Kalat, 1971; Shettleworth, 1972). So what are the general arguments concerning parallel systems of learning and memory, and what are the criteria by which this question should be judged?

The modular view of cognition (Fodor 1983) assumes that the brain possesses separate processing pathways dealing with information with different computational requirements. These modules are characterised by being informationally isolated. Only the output of a module is available to other processes. If the input to a module was ambiguous and the output is incompatible with that of other modules, processing may start again with altered input. However, intermediate stages of processing are not accessible and cannot be influenced by information other than the normal input to the module, even if that information should be relevant. A module's computations may or may not involve learning. Modules are assumed to perform their computations in a unique context. A structure that performs a specialised operation and is replicated as a subunit in different processing pathways, or a structure that is called up sequentially by different pathways to perform its operation, as a subroutine in a computer program may be called up, would not be considered a module. Modules may be served by a common memory system and retrieval mechanism or by separate memory systems.

Sherry and Schacter (1987) suggested that functional incompatibility should lead to the evolution of multiple memory systems. Functional incompatibility exists when an adaptation that serves one function cannot effectively serve another function due to different requirements for the solution of the two problems. Multiple memory systems are said to be characterised by fundamentally different rules of operation. Sherry and Schacter outline a strong and a weak version of this idea. "*By the strong*

*view, a memory system is a functionally autonomous unit in which the component processes interact exclusively with one another and operate independently of other such units. In this scenario different memory systems not only operate according to different rules but also share no component processes. By the weak view, a memory system is an interaction among component acquisition, retention and retrieval processes in which any of the components can interact with processes outside the system. In this scenario different systems share some components but are still defined by specific interactions among the processes that make up the system*".

The authors convincingly argue that an evolutionary analysis is applicable to memory because it fulfils the two essential requirements: heritable variation and effects on reproductive success. Heritable variation has been demonstrated in Drosophila and transgenic mice (Dudai et al., 1976; Silva et al., 1992). Several examples show the importance of memory for reproductive success. In some species predator recognition is mediated by observing the mobbing behaviour of conspecifics (Curio et al., 1978). Dominance hierarchies, which spare both winners and losers the costs of fighting in every encounter, rely on individual recognition. Altruistic behaviour is only an evolutionary stable strategy if restricted either to kin, who are likely to share that genetic predisposition (the inclusive fitness model of Hamilton, 1964), or to individuals who return favours (Trivers, 1971) and so also requires remembering individuals. One of the most striking examples of the need for memory comes from the study of food hoarding. It was originally assumed that food hoarders did not remember the locations of their hoards, found them with no greater success rate than other conspecifics and benefited from their own hoarding as much as from that of others. Then Andersson and Krebs (1978) showed that hoarding was only evolutionarily stable if the hoarding individual benefited more than others. The only privileged information that is not available to conspecifics, and therefore capable of providing that individual benefit, is memory. Since then food hoarding species have been shown to rely on memory rather than other strategies (Cowie et al. 1981).

The basic preconditions for evolution do apply to memory. What remains to be shown is a requirement for different memory systems and a plausible way of achieving diversification. The example chosen by Sherry and Schacter to illustrate functional incompatibility is the comparison between song learning and food cacheing. The arguments are that

(a) restrictions on what is learned would mean that only certain classes of spatial locations could be remembered,

(b) a sensitive period would mean that only cache sites established at certain times could be remembered,

(c) if memory were resistant to modification cache sites could not be forgotten and birds would persist in visiting emptied cache sites.

In each case the assumptions underlying the argument can be questioned:

(a) It is taken for granted that a cache site is analogous to a song. Only then would restrictions on learning mean a restriction on the cache sites that can be remembered. An alternative possibility is that the type of cue chosen to characterise a spatial location is restricted. Cheng (1986) suggested that only geometric parameters are used to specify a location. Brodbeck (1994) found that a food storing species in a delayed matching to sample task gave most weight to global spatial cues, less to array based spatial cues and least to the appearance of feeding stations, while a non storing species in the same task had no preference. Predispositions to associate certain classes of stimuli, such as taste with illness, can be accommodated by associative learning theory (Revusky 1977).

(b) In imprinting the appearance of a sensitive period, defined as the time during which learning can occur, seems to be an consequence of the imprinting process itself (see Bolhuis 1991 for a review). On the other hand, if sensitive periods are a consequence of developmental changes the concept cannot be applied to memory for cache sites in mature individuals.

(c) To counter this argument one need only assume that the bird remembers not only the cache site but also remembers emptying it. That birds do not simply forget empty caches is shown by the finding that birds avoid cacheing in areas where their caches have been pilfered.

Sherry and Schacter also suggest a functional incompatibility between a Memory System I, which is "procedural", "habit", "taxon" or "semantic" memory and Memory System II, which is "declarative", "locale" or "episodic" memory. The characteristic feature of tasks performed by System I is the requirement for detection and preservation of invariances across episodes, while System II has to preserve variances to create a unique representation of each event. Even this might be adequately described within a generalised associative learning framework by assuming a difference in a learning rate parameter. A low learning rate would allow recurrent features to overshadow rarely occurring features, detecting invariance. A learning rate high enough for one trial learning would lead to recall of all features of an event,

with associative strengths apportioned proportional to the salience of each feature. This would preserve variance.

The major problem with Sherry and Schacter's emphasis on different rules of operation is that they do not give a sufficiently precise description of what differences cause functional incompatibility. They do not offer a convincing argument that there are differences in task requirements that cannot be accommodated by parametric variations. That may be due to the examples chosen (imprinting, song learning, learning of stellar configuration and olfactory orientation in salmonids). Their most striking feature is that none is concerned with predicting a sequence of events. They might be better characterised as perceptual learning, though Bolhuis (1991) argued, in the case of imprinting, that the differences between an associative and a perceptual learning account may not be substantial. The argument for functional incompatibility would still apply if parametric variation cannot be accommodated within a single memory system, but Sherry and Schacter have not shown that this is the case. They do point out that, strictly speaking, it is only possible to determine whether there is functional incompatibility between two systems after a complete analysis of both, in which case the concept does not contribute to analysis. They suggest that functional incompatibility can nevertheless be useful by helping to refine hypotheses about memory systems.

If the question is whether there are multiple distinguishable memory systems, then the emphasis on rules of operation is not the most appropriate level of analysis. For example, classical and operant conditioning are dissociable. They can be made to have opposite effects through omission contingencies (reviewed in Mackintosh, 1983) and were shown to be independent in Holman and Mackintosh's (1981) blocking study. This implies that operant and classical conditioning depend on independent memory systems, yet there seems to be not even a suggestion that they operate according to different rules. Performing different computations would be a sufficient condition for the evolution of independent memory systems, but not a necessary one. Another condition might be that some data streams are best kept separate, Fodor's criterion of informational encapsulation, which could follow from parametric variation. In the context of memory Systems I and II, a low learning rate in an associative system would detect statistical invariance. A high learning rate would preserve variance, but to avoid forming a large number of spurious associations selectivity would be needed. High learning rates must be restricted to channels where events occur only rarely. If interference is minimised, possibly

through associative predispositions and context-specificity, learning is possible after few or even one event, or over relatively long delays (Revusky, 1971).

I have one final criticism of Sherry and Schacter's review. They argue there is a need for adaptive specialisation, but do not offer a plausible scenario for specialisation that would leave the original function of a memory system intact. They only offer a mechanism for specialised systems to become more generalised. This would imply an overall evolutionary trend from many specialised memory systems to few generalised systems. The process Sherry and Schacter suggest for generalisation could cause specialisation with only one additional assumption. Exaptation or preadaptation exists when a feature selected for a function A deals with that function in such a way that, by chance, it is of some use for some other function B that may become relevant later in the species' evolutionary history. Sherry and Schacter suggest that by this process specialised memory systems will be coopted to deal with new problems and become more generalised. However, if a feature is duplicated, as is the case with the various forms of haemoglobin, then a mutation in one of the two copies opens the way for differentiation. Worden (1991) suggests the hippocampus contains multiple "fragment fitters" operating in parallel. That would provide a possible substrate for more specialised memory systems, should the need ever arise.

Shettleworth (1993) argues that there is no single solution to the problem of classifying memory processes and that most discussions of the topic "rely on implicit pretheoretical assumptions, neither well justified nor consistently applied, about what differences among learning phenomena are important". It is necessary to recognise that learning phenomena might differ in a number of ways and that all learning is specialised in some way. A neat division into general processes and specialised adaptations is not possible. Consideration of how learning processes differ is therefore more profitable than disputes over how fundamental any difference may be.

Learning processes may be classified and compared along any of the following dimensions. The identity of the events responsible for learning and their specific effects of behaviour: the association of taste and illness leads to avoidance of the last novel food consumed while a suitable exteroceptive stimulus followed by a painful stimulus will trigger one of the predator avoidance responses. The conditions of learning: contiguity and contingency, relative salience, redundancy of stimuli, as in blocking, the relative novelty of stimuli, similarity between CS and US, ISI and ITI, etc. The contents of learning: what aspects of a situation are represented, details of stimulus features, emotional significance, timing, location? The structure of the

representation: associations of stimulus, response, outcome or some combination thereof or perhaps a change in a representational structure that cannot be reduced to associations? And finally, how does learning influence behaviour? A stimulus-response association need only activate the response. A stimulus-outcome association needs some mechanism to translate learning into performance. A cognitive map needs at least a readout mechanism. If learning can differ along all these dimensions, then obviously it can be specialised in each of these aspects.

Shettleworth then proposes that this bottom-up approach must be complemented by a top-down approach. A consideration of function can guide both the search for and the characterisation of specialised processes. In turn, specialisation can make it easier to give a rigorous and quantifiable definition of function. The study of a specialised process may then uncover principles of operation that also apply to general processes, whose specific parameters can then be understood in terms of their function, rather than appearing arbitrary. This relationship between function, or the goals of computation, and algorithm is one of the topics of the next section.

## 1.10. The representation of variability

Animals live in a world of uncertainty. They normally do not have complete knowledge of their environments, or even of the parts that are relevant to them. Even if they had complete knowledge, some events may be stochastic, rather than deterministic. Under these conditions animals can only make a best guess given available information. It may be valuable to know just how good this best guess is in order to assess the risk of acting on that information. A squirrel or bird should know the carrying capacity of a branch before attempting to land on it. Branches that appear identical to the animal will have a capacity varying about some mean. If beech branches have greater variance than birch, then allowance must be made for a greater safety factor.

Sensitivity to variability has been investigated in studies of event magnitude and timing. Comparison of stochastic and deterministic models of optimal foraging showed that optimal policies are different when animals have complete knowledge of invariant factors compared to when there is stochasticity of energy intake rate (Caraco, 1980; Oaten, 1977; Oster and Wilson, 1978; Real 1980; Stephens, 1981). Whether it is better to avoid or prefer a variable resource depends on the animal's situation. Stephens (1981) showed that the influence of variability on risk of starvation depends on the expected mean rate of energy gain during foraging. If the rate of energy intake is above the rate required to prevent starvation, the forager

should chose, among two food sources with equal means, the less variable one. However, if the rate is below requirement and reserves are low, then the more variable source offers a better chance of getting lucky (Fig 1.1). This reversal from risk-averse to risk-prone behaviour has been found in several studies (Caraco, 1981, 1983; Caraco et al., 1980; Stephens and Paton, 1986). Taking reproduction into account changes the optimal strategy again. If an animal's energy intake is sufficiently above requirement that starvation risk is low, but reserves are not sufficient for reproduction, switch to a risk-prone strategy offers a better chance of reproductive success (McNamara et al., 1991).

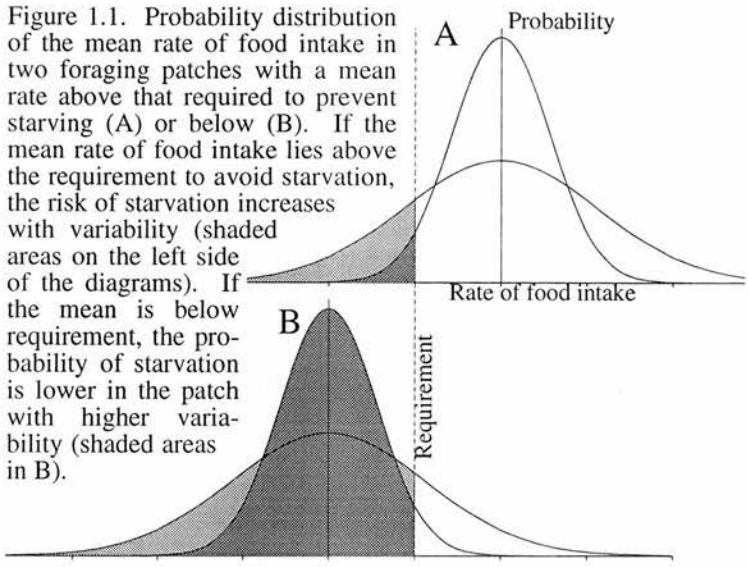



Figure 1.1. Probability distribution of the mean rate of food intake in two foraging patches with a mean rate above that required to prevent starving (A) or below (B). If the mean rate of food intake lies above the requirement to avoid starvation, the risk of starvation increases with variability (shaded areas on the left side of the diagrams). If the mean is below requirement, the probability of starvation is lower in the patch with higher variability (shaded areas in B).

Finally, it should be noted that sensitivity to variability of magnitude only benefits an organism if the number of samples it can take is limited, for example in the case of a small bird that must have sufficient reserves to survive the night. If the number of samples is very large, the energy intake rate approaches the mean regardless of variations. Honey bees send out a large number of foragers, each of which visits a large number of flowers, and were found not to show risk-sensitive foraging (Banschbach and Waddington, 1994).

Risk sensitivity has also been studied in the domain of the timing of events. Animals prefer small imminent rewards over larger delayed rewards. If the interval between small rewards is sufficiently short to give a higher rate of delivery, this is predicted by the matching law (Baum and Rachlin, 1969; Herrnstein, 1961), which states that animals match the proportion of investment into a resource to the relative rate of return it provides in comparison with other resources. Kagel et al. (1986) review evidence that animals often discount delayed rewards more than required by the matching law. As a consequence, if both reward size and average rate of delivery are identical in two patches, animals tend to prefer the patch with more variable timing. This tendency increases the lower the animal's energy reserves are, as long term gains are less important if the animal is too weak to pursue them. The temporal

discounting beyond matching could be considered an adaptation to uncertainty. In most natural situations an animal that goes for an immediate, but smaller reward has time and opportunity to search for more, while the animal waiting for the delayed and larger reward may lose it to a competitor, or may have to leave to avoid a predator. Thus in all cases where animals are "risk-prone" in that they prefer variability, the actual effect of this strategy is to reduce risk. This must be kept in mind when considering the functional significance of risk sensitivity.

Switching between risk-prone and risk-aversive strategies when dealing with the same variable is of special interest because associative learning is restricted to a single output variable. Explicit representation of both a mean and its statistical uncertainty is therefore presently beyond the scope of this approach. Is there some way of taking risk into account without explicit representation of statistical error? In the first example animals could give more weight to experience with weaker branches. This lowers the estimated strength of beech branches compared to the true mean (Dickinson, pers. comm.). Likewise, a bird whose expected reserves at the end of the foraging period will be above the requirement for avoiding starvation could give more weight to small amounts of reward found in a foraging patch, one below requirement more weight to large amounts. This strategy is possible only if two preconditions are met. First, the animal must have sufficient time to experience the conditions that require discounting one way or the other. If two different learning histories give rise to the same associative strength, the organism has no way of distinguishing between them. This is one of the most basic constraints of associative learning. Therefore it is impossible to distinguish between an associative strength based on experience of an invariable mean or a higher or lower discounted mean. If the required direction of discounting changes, this is only possible by new learning under these conditions. This precondition is not always realistic. A squirrel or gibbon on a foraging excursion will only aim for branches with an estimated strength above the required, and chose the lower variability given the same expected strength. If pursued by a predator, and given as the only possibility of escape a choice between two branches of equal expected strength below requirement, the better choice is the more variable one. This is one example where immediate reassessment is necessary. In the experimental studies of risk sensitive foraging it is not clear whether transfer between risk-prone and risk-averse behaviour is immediate when energy intake crosses over to the other side of requirement. The data of first choices are not reported. This means it is impossible to decide whether the animals explicitly

represented variation in reward magnitude, or whether they used nonlinear and deprivation dependent discounting of reward magnitude.

The second precondition is knowing which direction of discounting is appropriate. This is not a problem in the two examples above, the estimations of magnitude and timing. In the first case the appropriate strategy is defined by the animal's energy requirement compared to its intake, both variables available from monitoring its internal state. In the case of timing, the interruption-of-foraging account predicts only preference for resources with variable timing. Space presents a different problem, as illustrated by two examples of sensitivity to uncertainty in human marine navigation. When approaching a coast it is common practice to head to one side of the destination by slightly more then the estimated error. On reaching the coast out of sight of the destination it is then known in which direction it lies. It is not possible to discount the estimate of the direction actually taken because it is not possible to know in advance whether accumulated random errors will take the ship right or left of the destination. Before the development of sufficiently accurate and reliable clocks, celestial navigation gave a far more accurate estimate of latitude than longitude. When headed for an island, ships would steer for a point on the same latitude, but directly east or west by a distance exceeding the expected error in longitude. Discounting of direction is not possible for the same reason as before. If the error is in two dimensions of movement, not bounded by either a coast line or a latitude, a knowledge of the likely navigation error can serve a different function. Assume a fisherman returns to a lobster trap. If it cannot be found within the radius of estimated navigation error, the fisherman can give up and get on with other jobs. The same would apply to any animal searching for an impermanent and inconspicuous resource.

I have offered specific examples where explicit representation of statistical uncertainty would be advantageous. More generally, access to such an explicit representation offers greater flexibility. If the significance of a variable changes, as in the case of variability when requirement crosses over to the other side of the mean, an explicit representation allows to make that inference without further learning in that situation being needed. It also appears that space is different from time and magnitude in that discounting to take account of error is not possible even within limited cases.

To my knowledge uncertainty in navigation has not been studied directly in animals. However, some features of animal navigation may be considered

adaptations to uncertainty. In triangulation experiments systematic errors in dead reckoning take animals back not directly to the starting point, but make the return path intercept the outward path (Séguinot et al., 1993; see also Maurer and Séguinot, 1995; Etienne et al., 1996). Presumably that gets them back to an area they have just traversed and which should be familiar. Without this systematic bias, random errors would be more likely to take them into unfamiliar terrain. A similar principle underlies the desert ant's search pattern in the vicinity of the calculated position of its nest. The ant runs in loops that expand over time, but always return to the point where search was initiated (Wehner and Srinivasan, 1981). Search time distribution is a two dimensional Gaussian. The loops centered on the ant's best guess of the nest location allow error correction if the ant misses and comes near the actual location for a second time. Studies that have some bearing on the subject of error estimation in navigation will be discussed later in connection with landmark stability and in chapter 3.

## 1.11. Summary

The manipulation of a representation allows organisms to derive information about the environment that is not directly available in current sensory input. Representations can differ in the richness of isomorphism between represented relations and those in the environment, as well as in the range of inputs over which the representation is at least approximately isomorphic to the represented system. The basic assumption of associative learning is that several relations in the environment, such as correlation, average magnitude, timing, location and their variability, are compressed into a single output variable, the associative strength. Different learning histories leading to the same associative strength cannot be distinguished because no record of individual events is kept. Greater flexibility could be achieved by separate representation of each variable and their combination in ways appropriate to each situation. What is appropriate can only be determined after careful analysis of the problems posed by the environment. In the case of navigation that problem is how to reach a location of interest. Several strategies of varying complexity are possible, from trail following over chaining of actual or virtual beacons to vector navigation and the use of maps.

# 2. Strategies and models of navigation

This chapter deals with only a subset of the strategies derived in section 1.5 from a consideration of the possible function of a navigational system. The focus is on those systems that are obviously not straightforward in their use of cues. For example, trail following and the approach of beacons only require the recognition of and orientation towards the appropriate cues. Although continued recognition of a beacon as it changes size and appearance during approach may be complex, the navigational aspects of these strategies are too simple to be of interest here. Chains of S-R associations rely on recognition of a stimulus configuration and execution of an orientation and displacement response. They must either send the animal on a ballistic movement that only stops when the next stimulus configuration in the sequence is recognised, or else depend for appropriate displacement on the metric of internally generated cues. The arrangement of landmarks is only used to recognise a place. Information about relevant action lies in the association with response. There is no question that associative learning can account for such a strategy and it is also relatively uninteresting as far as use of landmarks is concerned. Therefore this chapter will concentrate on strategies that use information from the arrangement of landmarks to either calculate a directions that takes the organism closer to the goal, or to compute the actual goal location, followed by various ways of using dead reckoning. These strategies are more interesting in terms of navigation, and the computations involved might be different from associative learning and are interesting in that context, too. The chapter will roughly follow the outline of navigational strategies given in section 1.5, from use of snapshots over metric information derived from landmarks to landmark maps and, finally, dead reckoning. Each discussion of a type of navigational system will be followed by an outline of some relevant experimental evidence. The division between landmark maps and those integrating both landmark information and path integration (discussed in the next chapter) is, to some extent, arbitrary.

## 2.1. The use of snapshots in finding a goal

The strategies using external cues and having interesting navigational aspects begin with the use of snapshots. An animal may have some measure of the mismatch between a remembered snapshot and the currently perceived surroundings. The goal could be reached by a biased random walk, with the probability of a random change in direction decreasing the faster the mismatch decreases. This would be analogous

ref?

to bacterial chemotaxis (Adler 1976), with the degree of mismatch serving as a signal in place of the concentration of a nutrient. If the change of mismatch can be measured directly, the animal can move in the direction that decreases mismatch fastest.

Alternatively, the mismatch function could include a spatial component. Cartwright and Collett (1983) conducted a series of experiments investigating what properties of landmarks honey bees use to find an inconspicuous food source and how they use this information. Cartwright and Collett developed five algorithms to simulate the bees' behaviour. Only the one that provided the closest match will be described here. The retinal image and retinal snapshot are modelled as light and dark areas on a circle (Figure 2.1). The snapshot must be aligned with the compass orientation in which it was taken. Collett and Baron (1994) found that bees likewise adopt a stereotyped orientation during the last phase of approach to the goal. The middle of each area on the snapshot is determined and paired with the middle of the nearest corresponding area on the retinal image. This may lead to some areas being paired with more than one other, other areas may not be paired at all. The two variables that the algorithm attempts to match are orientation of areas and their angular extent. If paired areas are misaligned the algorithm generates a unit vector tangential to the retina such that movement in the direction of the vector would reduce discrepancy. If there is a mismatch in angular extent of paired areas, then the

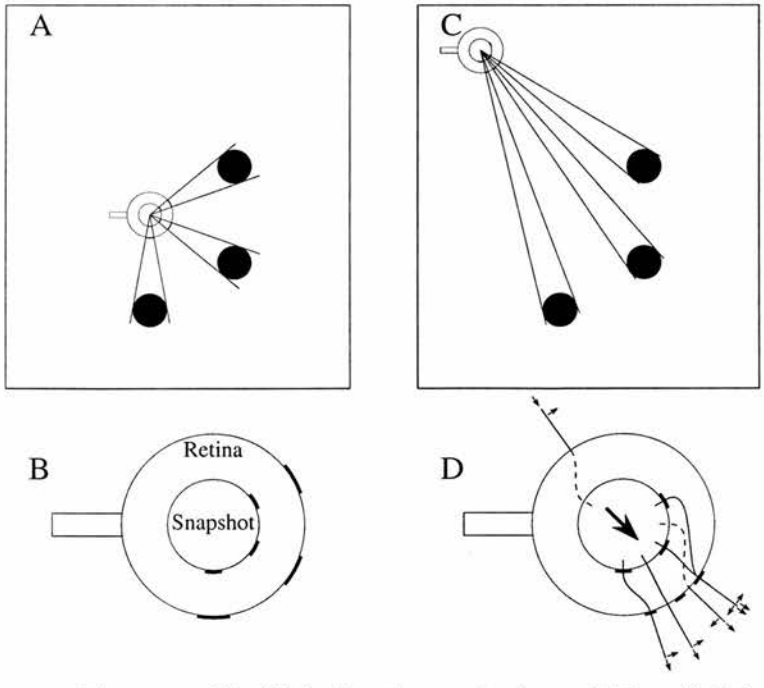



Figure 2.1. The snapshot model of Cartwright and Collett (1987). (A) The bee learns a snapshot at the goal. Landmarks are black discs. (B) The nner circle is the snapshot, the outer circle the current view on the retina. The bee's orientation, marked by a tail, remains constant. (C) Approach to the goal. (D) The bee matches areas on the snapshot with the closest areas on the retina that have the same colour. It flies towards areas that are smaller than remembered (in this case landmarks and the two gaps between them) and away from areas larger than remembered (the region without landmarks behind the bee). This is shown by radial unit vectors. If an area is farther right than remembered, the bee flies to the right, as shown by tangential vectors. The flight direction results from addition of all these unit vectors. The length of unit vectors does not vary with the size of mismatch. Adapted from Cartwright and Collett (1987).

algorithm generates a vector radial to the retinal bisector, pointing from the larger to the smaller area. The lengths of the vectors are not related to the size of the discrepancy. Addition of these vectors yields the flight vector. This vector does *not* represent distance and direction to the goal. It merely points in a direction that takes the bee closer to the goal.

An important feature of the snapshot is that it represents space only implicitly and in a quite impoverished sense. A bee navigating by snapshot does not know where the goal is, only how to get there. It does not know the distance of landmarks from the goal, only their retinal sizes. It does not know the distances of landmarks from each other. It does not even know the angles between landmarks, but only their retinal coordinates, or the retinal sizes of the spaces between them. As a consequence, an animal navigating by snapshot reacts to transformations of landmark arrays in quite characteristic ways. Changing the distance of landmarks while keeping their retinal size constant cannot have any effect on the final search location. Changing retinal size of landmarks, by altering either the size of landmarks or their distance from the goal, while preserving their compass bearings has little effect. Any adjustment of search location would change the retinal coordinates of landmarks even more, if the angles between them are larger than the angles subtended by the landmarks themselves. For the same reason a change of angles between landmarks would shift search location so that this angle was largely restored, even if that altered the retinal sizes of landmarks. Because snapshot algorithms only give a direction taking an animal closer to the goal, not even the exact direction of the goal, they require constant visual feedback. If an animal was given a view of a scene close to a goal and then deprived of visual input, it could not plan a route.

In the experiments that led to the development of the snapshot model, bees searched for food marked by one or several landmarks in a white painted room, measuring 4 m by 4 m. The position of the landmark array was varied systematically, but its compass orientation relative to reward was usually kept constant. First, bees were trained to search for food at three different distances from a single landmark. They concentrated their search at a single location near the landmark, not in an annulus around the landmark. The search distance correlated with the training distance. There are three potential cues bees might use to determine their distance from a landmark: motion parallax, looming (the change in apparent size when moving towards or away from a landmark) and retinal size. Search behaviour was most consistent with the use of retinal size as distance cue. Separate manipulation of

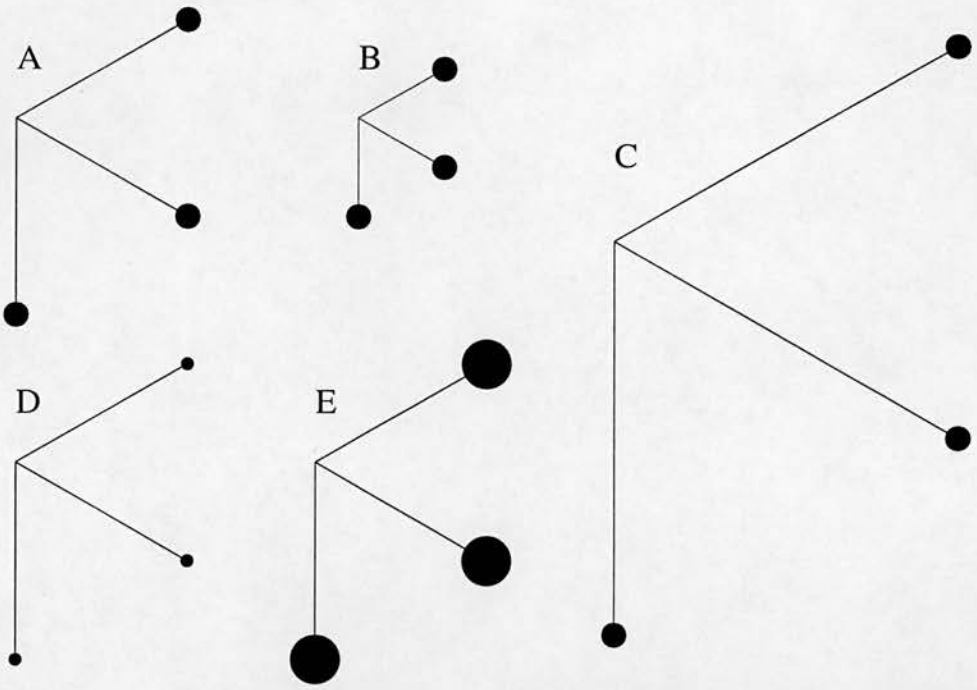



Figure 2.2. Navigation by snapshot in honey bees. Bees were trained with an array of three landmarks (A). The search peak is at the intersection of the three lines. Its location was not influenced by halving (B) or doubling (C) the distance between landmarks and goal, nor by halving (D) or doubling (E) landmark size. Adapted from Cartwright and Collett (1983).

the vertical and horizontal extent of landmarks showed that both are used to determine distance.

When the bees were trained with an array of three landmarks their behaviour was best described by the simple rule that they moved until the compass bearings of the landmarks were correct. Given a choice between a location where either the distances or the compass bearings were the same as during training, the bees preferred to match compass bearings. Altering the size or distance of landmarks did not change the location of search (Figure 2.2). Landmark size is not completely ignored. When the middle landmark was removed there were three possible partial matches of compass bearings. The bees chose the one that also matched landmark sizes. After a rotation of the array of 30° relative to the training orientation the bees still searched at the location specified by the angles between landmarks. If the array was rotated 90° the search location changed. Training with arrays of varying orientation had a similar consequence. If the array was allowed to assume any orientation during training the bees searched indiscriminately over a wide area. If the training orientation varied no more than ±45° from the orientation during the tests, the bees searched in the area specified by interlandmark angles.

The bees accepted imperfect matches between training and testing location. To

test whether they were at all sensitive to the fact that matches were sometimes not perfect, they were trained to find food in a square, at the intersection of the diagonals. The comparison array was a rectangle with diagonals of the same length as the square, but different angles between them. The more these angles deviated from 90°, the more the bees preferred the square. If the comparison array was kite shaped, which changed the distance of one landmark, but not the angles between diagonals, the bees showed no reliable preference for one array over the other.

Cartwright and Collett (1987) extended the applicability of the snapshot model to long-range navigation by adding several features. First, bees are assumed to use stacks or sequences of snapshots. As they fly from the hive to a feeding site they tick off one snapshot in the sequence after the other. Second, dead reckoning provides a rough estimate of the distance and direction from the hive of feeding sites and of locations where snapshots have been taken. This requires reading out locations from dead reckoning and storing them in long term memory. If a bee gets displaced it can pull out the best matching snapshot and either return to the hive or, if capable of vector addition, fly towards the feeding site. This will be discussed in more detail in chapter 3. Third, the bee computes goodness of fit between snapshot and current view. If all snapshots in memory fall below a threshold, it creates a new one. Finally, the bee filters landmarks according to distance. At any location it can create two or more snapshots by storing only landmarks within a certain range of distances. The arrangement of landmarks very close to a goal will not be recognisable at a large distance. Distant landmarks will not change their arrangement sufficiently when trying to pinpoint the goal. By filtering when the snapshot is created, and storing the filter setting so it can be used when matching the snapshot, the bee can adjust the accuracy and catchment area (where the output of the algorithm takes the bee closer to the goal) according to its needs. This does not require storage of distances of individual landmarks, only of the range in which landmarks will be accepted. Bees can determine distance through motion parallax (Srinivasan et al., 1989).

Cheng et al. (1987) provided evidence that bees weight landmarks according to their distance. Bees were trained to find food in the centre of a square array of four large blue cylinders . Two smaller yellow landmarks were close to the goal. When the bees were tested with the larger and more distant landmarks alone they searched in the centre of the square. When the smaller proximal landmarks were moved from the training position, the bees preferentially searched at the location defined by the proximal landmarks (Figure 2.3). When the distance between the arrays was large

there was a secondary peak in the centre of the distal array.

Further evidence for weighting according to distance comes from an experiment with a trapezoid array of two large and two small blue and yellow landmarks. From the goal the angles between adjacent landmarks and their apparent sizes were equal. In tests with either four small or four large landmarks in a rectangle the bees searched in the area that gave the best match of the two small and proximal landmarks, even when large distant landmarks better matched the training configuration. Weighting according to distance when the memory is stored overrides a possible influence of distance on matching.

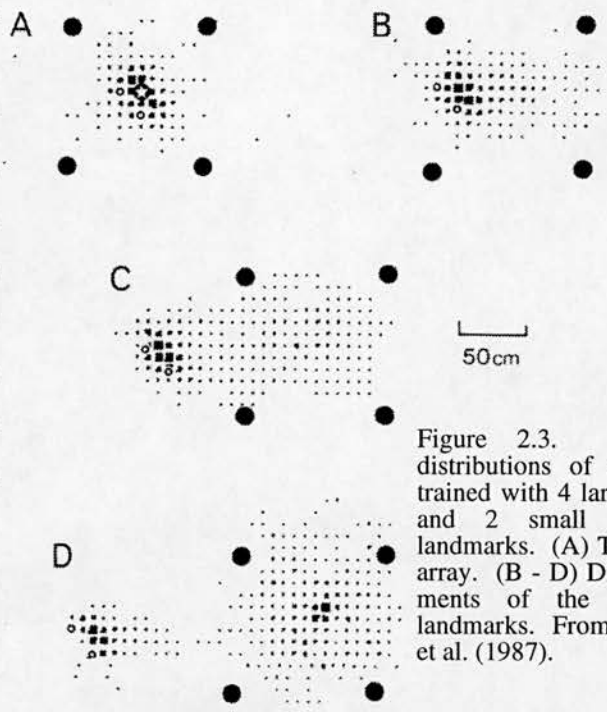



Figure 2.3. Search distributions of 4 bees trained with 4 large blue and 2 small yellow landmarks. (A) Training array. (B - D) Displacements of the yellow landmarks. From Cheng et al. (1987).

Bees also weight landmarks according to apparent size. They were trained to the centre of a square array of two small and two large landmarks. Tested with a stretched array they showed a preference for the goal location defined by the larger landmarks. When tested with the small landmarks alone they showed no bias to either side. With the large landmarks they had a strong bias towards the correct side.

In both cases the effect of differential weighting is more accurate definition of the goal. Closer landmarks change their bearings more for a given displacement. At a given distance the apparent size of a larger landmark will also change more than that of a smaller landmark.

Distance estimation from cues other than apparent size can contribute to matching memory and perception. Bees were trained with a trapezoid array of two large and two small landmarks, with equal apparent size at the goal. Tests were conducted with either only two small or only two large landmarks. If only apparent size contributed to matching, both partial arrays would give equally good matches on either side. The bees showed a small but significant bias in the correct direction in both tests. This matching by distance did not occur in Cartwright and Collett's experiment where one landmark of a square array was moved to produce a mismatch in both distance and

apparent size (see above). It is not clear whether in this case distance contributed to navigation, or whether it was merely another feature, like colour and shape, that contributed to matching landmarks to the snapshot. If bees can only use the remembered distance between goal and landmark, this knowledge is only useful for matching once the bee has reached a position with good correspondence between perception and snapshot. Using knowledge of distance from other locations effectively requires vector addition, which in turn would make snapshot navigation superfluous.

## 2.2. Metric information from landmarks - Vector navigation

The common feature of the navigational strategies discussed so far is that travelling to a destination not visible from the point of departure is only possible through route following. Despite increased flexibility, even the snapshot model does not allow to plan a route in advance, except by chaining snapshots. In the absence of metric information it is not possible to estimate the travel costs of novel routes. Cramer (1995, reviewed by Gallistel and Cramer, 1996) showed that vervet monkeys minimised route length by looking at least three locations ahead when planning novel routes in a familiar environment.

One possible representation of space that includes metric information is the storage of vectors between a destination and nearby landmarks (Collett et al., 1986; Cheng 1988). If there is some discrepancy between vectors, the animal is assumed to search at a spot that is the weighted average of all relevant vectors (Figure 2.4). In contrast to a snapshot algorithm, metric information enables gerbils to execute a route in the dark, after room lights have been switched off and visual feedback is no longer possible (Collett, 1987). Vector representations also react to landmark displacements in ways that are characteristically different from those of snapshot algorithms. As discussed above, snapshots tend to minimise deviations from the remembered angles between landmarks or their compass bearings. When a landmark in an array is

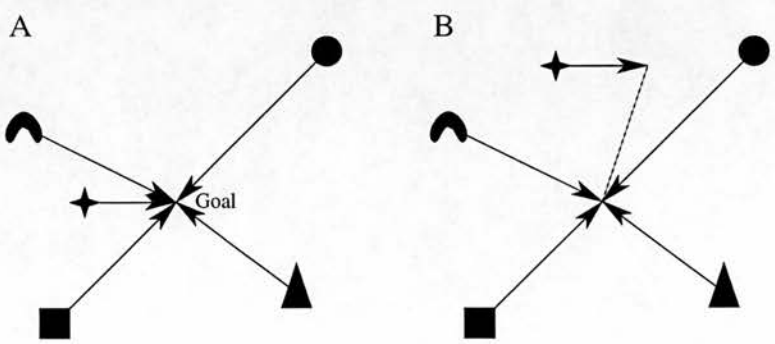



Figure 2.4. The vector sum model. If a landmark is moved its landmark-goal vector moves with it. Determining the goal location by a weighted sum of vectors results in a search location on a straight line between the tip of the displaced vector and those of the other vectors.

moved, the search peak typically shifts not only in the direction of the landmark displacement, but also perpendicular to it. If a destination is specified by landmark-goal vectors, the effect of landmark displacement is quite different. As a landmark is displaced, the corresponding landmark goal vector moves with it. If no other vector moves, the weighted vector sum must lie on a line between the end point of the displaced vector and those of all other vectors (Figures 2.4 and 2.6). If landmark identity can be established reliably on the basis of their appearance, only landmark-goal vectors need to be stored. If some landmarks cannot be distinguished by their features, as is likely in natural situations, they must be identified by their spatial relations to other landmarks. The possible number of vectors between N landmarks is (N-1) + (N-2) + ... + 1, or $N^2/2 - N/2$. If all possible vectors between a large number of landmarks were stored, this would lead to a combinatorial explosion. If spatial relations are explicitly represented in the form of vectors, one might expect that only those vectors necessary for a task would be stored to keep memory load low. The acquisition of information should be goal driven, in contrast to O'Keefe and Nadel's characterisation of a map, which can be curiosity driven due to its efficient storage scheme. Of course, like all efficiency arguments, this must be treated with caution.

## 2.3. The use of individual landmarks in mammals and birds

Collett et al. (1986) conducted a series of experiments on landmark use in gerbils. The results suggest that when gerbils are faced with discrepancies between training and testing conditions, they do not compute a single best match based on global parameters, but they use landmarks individually to find possible matches. Gerbils were trained to search for a sunflower seed at a location in a circular arena, specified by one or more landmarks.

In the first experiment the seed was hidden 50 cm in a consistent compass direction from a single, rotationally symmetrical landmark. The landmark alone cannot specify a point location, but only a distance. Nevertheless the gerbils searched for food at a single location, roughly at the correct distance. They must have had other directional information (see discussion of Etienne et al. 1986).

Gerbils can use a consistent direction between the start point and an array of landmarks and goal as a directional cue. When the whole arrangement of start box and landmarks was rotated and the distance between start box and landmarks was varied, the gerbils ran straight from the start to the goal. If the start direction was varied relative to the centre of the array, the subjects seemed lost and searched widely

in the vicinity of the array. After further training with varying start positions the gerbils searched in the appropriate position regardless of the start location. The same animals were then trained to search for the seed when the light was switched off during their approach, at a point 100 cm to 250 cm from the goal. The search distribution was still centred on the goal, evidence that gerbils can plan a trajectory and execute it without constant visual feedback. There were several controls for spurious cues.

The results of experiments involving alterations of the array suggest that the landmarks were used individually to determine the location of the goal. Gerbils were trained to a goal in the centre of an equilateral triangle of identical landmarks. When tested with only one landmark, they searched in three separate locations, each corresponding to a different match of the remaining landmark to one of the three in the array. With two or three landmarks there was only one possible match and search was restricted to one location.

Another group received training with a seed placed to the south of two identical landmarks (Figure 2.5). In tests with both landmarks search was concentrated on the goal location. When one landmark was removed, the remaining one was matched to either landmark in the array, generating two search peaks in the compass directions appropriate for each match. There were also two search peaks when the distance between landmarks was doubled. The gerbils' search was not determined by the compass bearings of landmarks, as for honey bees. They searched where the distance and bearing from individual landmarks were correct. Relations between landmarks are taken into account when identifying landmarks. The landmarks in the stretched array were correctly matched to the eastern and western landmarks in the original arrangement, else each landmark should have generated two peaks.

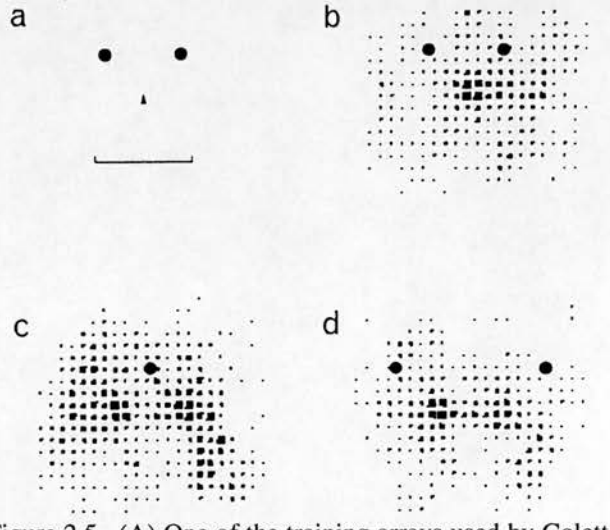



Figure 2.5. (A) One of the training arrays used by Colett et al. (1986). The landmarks are shwon as black circles, the food location is marked by a small triangle. (B) Search distribution during tests with the original array. (C) When tested with landmarks there were two peaks at the bearings and distance appropraite for each landmark. (D) When the distance between landmarks was doubled there were also two peaks.

The gerbils were also capable of using spatial relations between landmarks to obtain directional information or discriminate arrays.

Some animals were trained to find reward in the centre of an equilateral triangle of identical landmarks kept in a consistent orientation during training. A test with the array in the training orientation resulted in search concentrated in the centre. When the array was rotated 60° the animals soon left the centre and searched at three locations outside the array, producing a large central and smaller peripheral peaks. This is consistent with the animals searching at goal locations defined by individual landmarks. The same animals were then accustomed to approaching the array in the dark. In subsequent tests they always searched in the centre. This implies that the trajectory was planned using directional information from the array. Gerbils were also found to be able to distinguish between arrays of identical landmarks arranged either in an equilateral or scalene triangle.

These experiments show that gerbils have a spatial representation which either explicitly contains or allows to recover information about the distance and direction of a goal relative to landmarks. Gerbils' ability to complete a trajectory in the dark also demonstrates that distance must be represented in a form that makes it possible to compute the length of a trajectory. Directional information can be derived from from properties of the array or other unspecified cues. Given the choice between two arrays differing only in their orientation, the gerbils prefer the one that matches the training orientation. The search pattern in tests with rotated or distorted array is consistent with landmarks being used individually to specify the position of the goal. Landmarks cannot be treated independently when an array must be identified on the basis of the spatial relations between landmarks. Addition of vectors between current position, landmarks and goal specifies a trajectory to the goal. When different vectors point to different locations, a goal may be determined by computing a weighted average, analogous to computing the common centre of gravity of several masses. Vectors from landmarks close to the goal are given more weight. The data do not allow to decide whether spatial knowledge is explicitly represented as a list of vectors or whether the vectors are recovered from some other type of representation.

Further evidence for the use of weighted vectors, as well as quantitative data, comes from a series of studies by Cheng (1988, 1989, 1990, 1992). He trained pigeons to find food in a well, hidden under bedding in a square (160 cm by 160 cm) enclosure close to one of the walls (Figure 2.6). During training a light blue cardboard cue was mounted on the top wall, centred 50 cm from the right wall. Search behaviour was analysed separately along up-down and left-right axes.

Initial control tests established that the search distribution in the absence of food

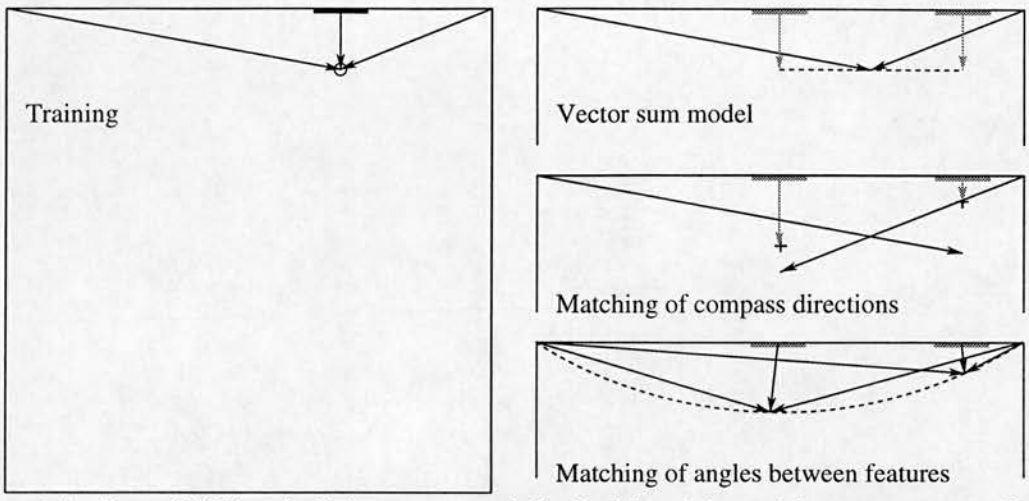



Figure 2.6. Cheng (1988) trained pigeons to search for food in a 1.6 m x 1.6 m square arena, 20 cm from a cue card on the "top" wall and 50 cm from the "right" wall. When the cue card was shifted up to 30 cm, the search peaks shifted only parallel to that movement. Matching of the compass directions of cue card and the two nearest corners would have resulted in search at the locations marked by +. When matching angles between cues, a perfect fit is possible for any cue card displacement, somewhere on the broken curve.

and food well was centred on and roughly symmetrical about the goal. In the presence of the landmark the peak was equally pronounced along both axes. Absence of the landmark did not affect search distribution along the up-down axis, but broadened the distribution along the left-right axis.

Displacements of the landmark along the wall only affected the search distribution along the left-right axis, parallel to the wall. The location of the search peak shifted with the landmark until an individual limit was reached, then remained at that limit. The slope of the variable portion of the displacement function indicates the relative weight of the vector between landmark and goal. An animal that only paid attention to the landmark would shift its search exactly as far as the landmark was displaced; the slope would equal 1. No attention to the landmark would lead to no displacement and a slope of 0. The relative weight given to the landmark stayed constant (shown by a constant slope through the origin) until a limit of landmark displacement was reached, then the weight decreased with further displacements. The spread of the search distribution increased along the left-right axis with landmark shifts along this axis. The search distribution along the up-down axis was unaffected. The data do not fit a model based on matching apparent sizes and compass bearings (Figure 2.6).

Cheng (1989) extended these results in a study with two landmarks in the same apparatus. The goal was located 20 cm from the middle of the top wall. The landmarks were rectangular wooden blocks which were placed 10 cm and 40 cm either side of the goal. In tests they were moved either parallel or perpendicular to

the top wall. The results broadly conformed to the previous study, with shifts and increases in the spread of the search distribution occurring only in the axis of landmark shift. In addition, the pigeons gave more weight to the closer landmark, consistent with Collett et al. (1986).

In the first experiment of a third study (Cheng 1990) a single wooden block, was placed either 15 cm or 30 cm to the right of the goal. The spread of the search distribution along the right-left axis was found to be proportional to the distance between landmark and goal, corresponding to Weber's law. Data from Cheng (1988) were reanalysed, confirming this result.

In the second experiment a landmark was moved diagonally, from 9 cm left and 8 cm down from the goal to 19 cm left and 18 cm down from the goal. The vector sum model predicts that a displacement of search should occur only in the direction of landmark displacement, due to the fact that the expected goal location must lie between the locations specified by displaced and non-displaced landmarks. The two birds tested with the diagonally displaced landmark showed significant shifts perpendicular to the direction of landmark displacement. This pattern of search shifts was replicated by Spetch et al. (1992) in a touch screen task, by Gould-Beierle and Kamil (in press) testing Clark's nutcrackers in an arena and by Cheng and Sherry (1992) with chickadees and pigeons.

Cheng argues that these result disconfirms the vector-sum model of landmark use. He does concede that in these experiments the landmark is relatively more informative about the goal position along the left-right axis, as it is much closer to the goal than any other cue. Along the up-down axis the next wall is a good distance cue. So a bird may only record that the goal is a specific distance from a vaguely defined part of the wall. Cheng claims that this is not a landmark-goal vector because it does not have a definite point of origin. Such a definition of a vector is appropriate when a landmark is small compared to the vector's measurement error. If a landmark is larger than this error, or even larger than the vector, then clearly the origin of the vector must be specified with respect to local features of the landmark or with respect to other landmarks. If these other landmarks are far away, determination of that origin will be inaccurate. In this example the location of a top-wall to goal vector could even have been determined partly by reference to the shifted landmark, and would have moved with it. Alternatively, the results could be described in terms of representations of distances and directions, with vectors decomposed into either distances and angles or into orthogonal scalar components.

The difference is more than semantic. Although direction is represented in the brain (Taube et al. 1990a, 1990b) the question arises whether these components are accessible to the animal when choosing where to search, or whether only the end result of the computation, complete vectors, is available. When landmarks and their corresponding vectors are displaced, these alternatives are indistinguishable. When vectors are given definite starting points, but their directions are altered, a distinction can be made (see Figure 2.7). Cheng (1994) used this principle in a series of experiments with pigeons. The direction of a vector was changed either by rotating a directionally polarised landmark, or by training with two landmarks indicating different directions, testing with one landmark and exploiting confusion between them. It was found that averaging of polar vectors, or of radial distance and direction separately, gave the better fit to the data. There is one problem with that conclusion. As the effect is fairly subtle, data from four experiments were used. In one of those experiments the landmark was placed in the centre of a circular tray, with food close to the edge of the tray. A vector pointing from the edge to the landmark would introduce distance from the edge into the averaging process, even if only whole vectors are averaged. Only if the result is not changed by omission of this experiment can Cheng's conclusions be accepted.

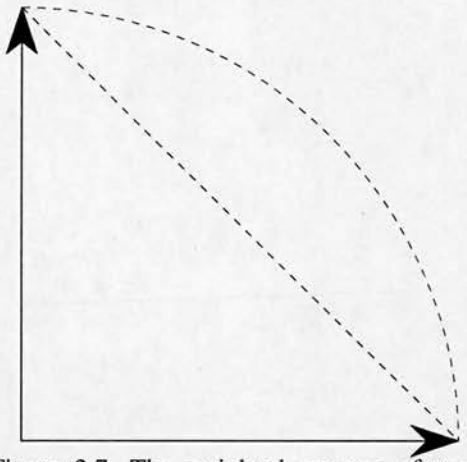


Figure 2.7. The weighted average of two complete vectors must lie on a straight line between their end points. The same applies to decomposing the vectors into orthogonal scalars and averaging then. If direction and distance are averaged separately, the resultant vector will have the same length as the two original vectors and the end point must lie on an arc of circle. Adapted from Cheng (1994).

## 2.4. Interactions between landmarks

Most of the data on interactions between landmarks cannot distinguish between vector navigation and use of a map. Many are silent even with respect to the distinction between snapshot navigation and navigation using metric information. Nevertheless, this section is included here, so that the description of mapping theories can be directly followed by the relevant data.

Suzuki et al. (1980) studied the role of extramaze cues in spatial learning in the eight-arm radial maze to compare the predictions of the cognitive mapping theory (O'Keefe and Nadel 1978) with those of the working memory model of Olton (1978). The maze was housed in a large cylindrical chamber to improve stimulus control.

Seven different stimuli hung over the ends of seven of the arms. The eighth arm was unmarked (Figure 2.8).

All animals were trained with extramaze stimuli present. They made three forced choices and were confined on the centre platform for 2.5 minutes, followed by free choices until the remaining five food pellets had been obtained. In control trials the array of stimuli was rotated by some amount and then rotated back during the confinement period. In rotate trials the stimuli were rotated and the arms rebaited accordingly. In transpose trials the stimuli were randomly rearranged, and five arms associated with stimuli which had not been chosen previously were baited. There was no difference between rotate and control trials, while performance was disrupted by the transposition. Two choices would be correct regardless of the cues the rat might use (Figure 2.9). The rats' choices did not differ in these arms with overlapping stimuli, but did differ between the transpose trials and the rotate and control trials in the three remaining arms, where extramaze stimuli and possible spurious cues provided different information. This indicates that the rats did not treat the extramaze stimuli as simple beacons, but used them as a configuration.

In a further experiment all arms were rebaited after the confinement period to test

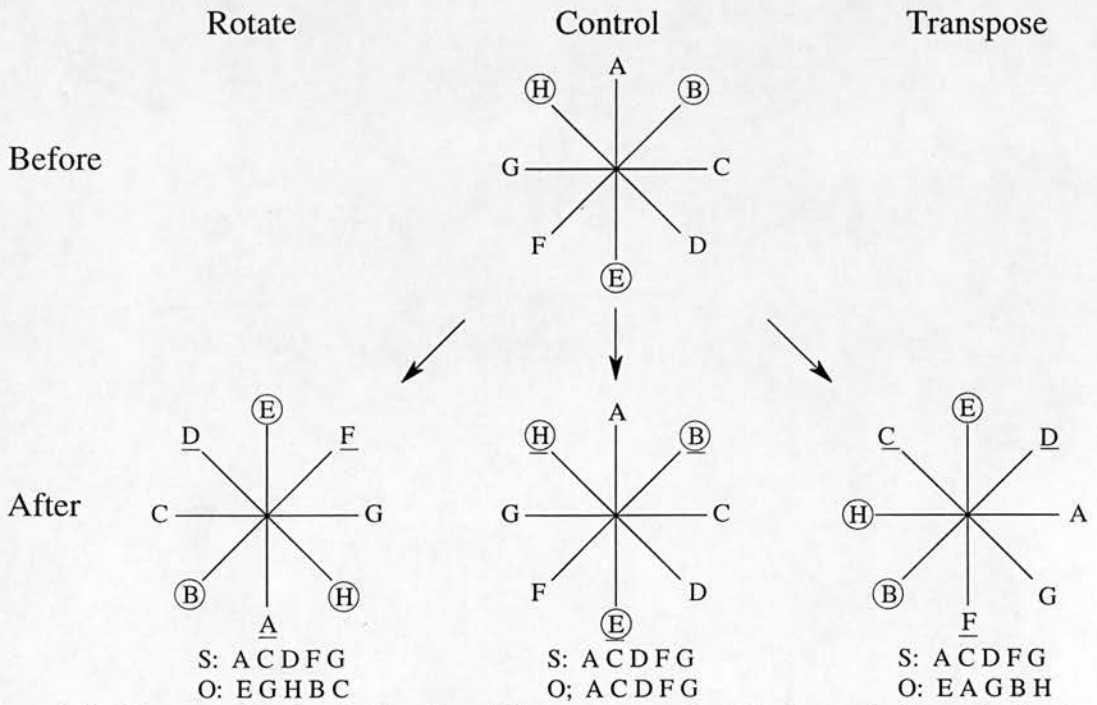



Figure 2.8. Diagrams showing the location of the extramaze stimuli before and after each stimulus manipulation. Encircled letters indicate the stimuli chosen in the forced choices, underlined letters their locations before the control and stimulus manipulations. Rats should choose the stimuli designated as S if they use the stimulus cues in guiding their performance, while they should choose stimuli designated as O if they rely on some other cues such as intramaze and extrachamber cues. Note that S and O are dissociated with two overlapping elements in both rotate and transpose trials. (After Suzuki et al. 1980)

whether memory might be reset during the confinement. If the rats did reset memory then, first, the number of different choices should be comparable to performance without preceding forced choices. Second, the choices after confinement should be unrelated to the forced choices. While the first condition was fulfilled after all three types of cue manipulation, only after a transposition did the rats fail to avoid the stimuli visited in the forced choices. Suzuki et al. took this to indicate that the free choices were treated as a new trial, unrelated to the preceding forced choices. An alternative interpretation is that the new configuration of stimuli was treated as a new environment. This assumption generates a different prediction from the working memory theory if "resetting" is taken to imply erasure of the memory of the forced choices. In that case the rats should choose unrelated to the three forced choices if the original configuration was restored after the free choices. If they treated the changed configuration as a different place, restoration of the original arrangement should lead to the rats avoiding the arms they visited in the forced choices.

Cheng and Gallistel (1984), intended to specify more precisely than Suzuki et al. (1980) what properties of the configuration of cues are contained in the rat's spatial representation. The experimental environment was designed to allow some categories of geometric properties to be manipulated independently. If the rats' performance was disrupted by conflicting information from two classes of properties than both classes must be contained in the representation, else the rats could not detect the conflict.

The geometries to be examined were selected on the basis of two assumptions. The first is that "animals may have weaker representations of space, but they are unlikely to have systematically wrong ones" (Cheng and Gallistel 1984, p 412). The geometries to be investigated therefore should be Euclidean geometry and those that can be derived from it by deletion of some properties. The second assumption states that weaker representations can be derived by deleting properties not in any arbitrary order: "*an imaginable neural code cannot capture formally stronger relations while failing to capture the weaker, more primitive relations*" (Gallistel, 1990; p. 176).

A hierarchy of relations can be developed by characterising them through the transformations that change selected sets of properties. Rotation and translation are Euclidean transformations. Coordinates change while the metric properties, congruence of line segments and angles as well as linear and angular distances, are conserved. Affine transformations are equivalent to uniform stretching and compression along arbitrary axes. Parallelness, ratios of distances within families of

parallel line segments and cross ratios of angles remain unaltered. Using only those and weaker properties no two triangles of any size and shape can be distinguished. A square can be transformed into any parallelogram, but not into a trapezoid or kite shape, as that would not conserve parallelness. Projective transformations conserve straightness, collinearity and type of conic section (ellipse, hyperbola, parabola). Considering only projective and weaker relations a kite shape could not be distinguished from a square. Topological transformations are arbitrary stretches and compressions. Only the concurrence of curves at a point is conserved. The hierarchy stems from the fact that a given transformation alters all stronger properties while conserving the properties of its own and all weaker classes. For example, a projective transformation alters Euclidean and affine relations and conserves projective and topological relations. The only relation that stands outside this hierarchy and can be included or excluded at any level is sense, the distinction between right and left.

The experimental environment was a rectangular box, 120 cm by 60 cm, with black walls. Four movable boards in the corners of the enclosure served as landmarks (Figure 2.09). An affine transformation can be achieved by squashing the enclosure, maze and landmarks by a factor of 2 along the long axis and stretching them by an equal factor along the perpendicular axis. An equivalent procedure is the

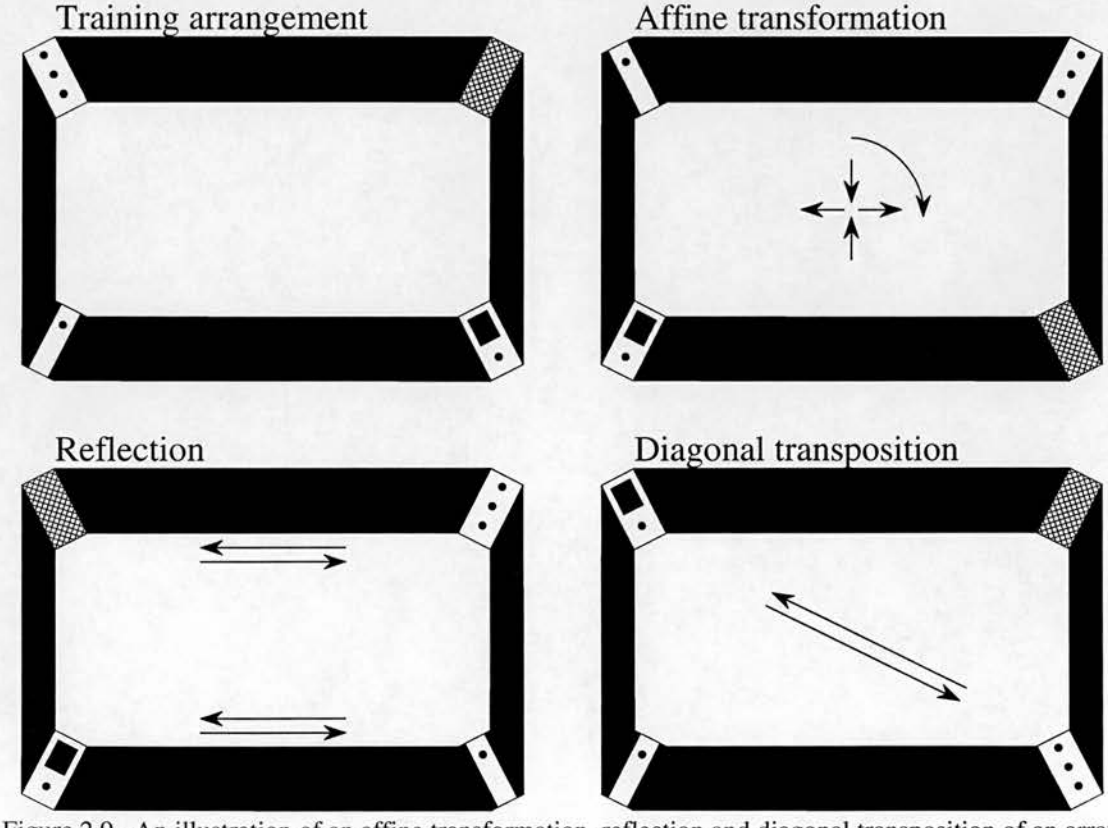



Figure 2.9. An illustration of an affine transformation, reflection and diagonal transposition of an array of stimulus panels (adapted from Cheng 1986)

movement of each cue to the adjacent corner either clockwise or anticlockwise. In all experiments the rats were isolated as well as possible from spatial information from outside the box. In a first study, rats' search for food in the corners of this arena was unaffected by a rotation of cues, while they were severely disrupted by both the reflection and the affine transformation. Cheng and Gallistel concluded that the rat's spatial representation must include both metric properties and sense. However, a more surprising feature of the rats' behaviour came to light when they later realised that affine transformation and reflection only test for metric relations and sense in isolation if rats relied primarily on the landmarks in the corners. If the rats only paid attention to whether the chosen corner has a long wall on the left and a short wall on the right, or vice versa, metric properties and sense are tested in conjunction, not independently. Either transformation moves a bait from a corner with a long wall on the left and short wall on the right to a corner with the opposite arrangement. On the other hand, such a representation does not enable a rat to distinguish between the two corners on the same diagonal. A reanalysis of the data and further experiments by (Cheng 1986) in similar rectangular boxes confirmed this second interpretation. Even covering one of the long walls with white polystyrene to give a very salient cue to break the symmetry did not improve performance.

To investigate whether rats were able to use featural information at all in this environment, some were trained in a reference memory paradigm. During the first test phase the enclosure contained corner panels and one white wall, in the second test phase only the four corner panels. Under both these conditions rats learned to choose the coorrect corner, though the rats found it easier to identify a geometrically correct corner than to distinguish between the two geometrically correct alternatives. In a third test the panels in the correct and the diagonally opposite corner were removed. In principle, the global congruence of cue arrangement could serve to identify the correct corner. However, while the rats still had a significant preference for the correct diagomal, they did not discriminate between the two alternatives. Cheng concluded that, first, featural information is discriminable, second, that the rats still rely to some extent on shape to identify the goal and third, that featural information in the geometrically correct corners was necessary for discrimination. Although, in principle, just one panel in one of the adjacent corners is sufficient to make a choice the rats could not use this information.

Finally, rats were unaffected by a diagonal transposition, an exchange of the panels in the correct and the diagonally opposite corner (Figure 2.9). It changes

distances and angles between cues and their cyclical order, but leaves the geometrical relations between the shape of the enclosure and the corner panels in the correct diagonal intact. Errors were, again, concentrated in the diagonally opposite corner. Performance declined in a second phase, when tested with either a reflection or an affine transformation. Errors were no longer predominantly in the diagonal with the correct panel.

Gallistel (1990) quoted another experiment which was not included in Cheng's (1986) paper. Between sampling and test phases of a working memory paradigm, the arrangement of stimulus panels always underwent an affine transformation. After the retention interval food was never in the same position as defined by Euclidean geometry, but was still under the same stimulus panel and in the same location as defined by affine geometry. The rats did not show any preference for either a stimulus panel or a diagonal. Gallistel argues that despite the increased difference between optimum performance using affine geometry (25%) versus featural information (100%), the rats fall back on affine relations to identify the goal, but still rely on geometrical information. An alternative interpretation would be that the rats learned two (or four) locations in which food could be found: one (or two) with the long wall on the right and the short on the left, and one (or two) with the long wall on the left and the short wall on the right. Either way, geometry was more important than the features of the panels.

Margules and Gallistel (1988) tried to test three hypotheses arising from these experiments. First, the assumption that the occurrence of rotational errors depends on the rats being disoriented with respect to the space outside the box. Access to information from a larger frame of reference should disambiguate geometrical information from the box. Second, if there is a conflict between the two frames of reference the rats should react to it, but may still be able to establish their heading if the smaller frame of reference is directionally polarised. Third, they hypothesised that the reason for the rats' failure to use featural information was that the corner panels were perceived as moving and therefore unreliable. This could happen if the rat, on finding itself misoriented 180°, assumed that not its orientation was at fault, but that the stimulus panels had moved. Training in an environment that avoided misorientation might make the rats rely on the cue panels.

The same two boxes served as experimental environment. While neither of two groups of rats was in any way isolated from the room in which the experiment was conducted, only one group was offered stimulus panels in the corners of the boxes.

Rats in both groups learned to find the goal equally well, without rotational errors. When the orientation of the box changed during the delay, performance dropped significantly. The groups with and without panels did not differ. In the next experiment the rats were isolated from sources of information outside the boxes. All rats were trained and tested with stimulus panels in the corners of the boxes. No rat distinguished the ends of the boxes. The two subjects previously trained with panels present did not have any advantage due to perceived stability of the cue during earlier training.

Gallistel (1990) drew the following conclusions from this series of experiments. He argues that there is a neural system which creates a Euclidean representation of space and distinguishes between right and left. It uses only geometric information, the shape of the environment, to establish the rat's location and orientation. Featural information is only used to check the result after a geometric congruence has been established and only local features, close to the goal, are taken into account. The system takes only restricted types of information, performs specialised computations and only the output, not intermediate stages of processing, are accessible to other processes. If the output must be rejected the system goes through the whole computation again, with altered parameters. It is informationally isolated or impenetrable, meeting Fodor's (1983) criteria of modularity. This geometric module has several scale of representation. If orientation, or possibly location, at one scale is ambiguous, information from a larger frame of reference may be used to orient and place the smaller frame of reference correctly. Shape is ignored at a small scale, such as texture or the holes in some of the stimulus panels, at least for the determination of orientation.

Gallistel offered arguments for impenetrability on both computational and evolutionary grounds. One argument is based on the computational properties of image alignment or template matching algorithms. Those algorithms may be divided into local correspondence and global parameter-matching algorithms. Local correspondence algorithms try to minimise the overall discrepancy between points or features (sets of points) in the two images or shapes. Unless there is at least one unique point or feature the algorithm may have to go through all possible translations and rotations until it finds the best match. Where time or computational resources are at a premium this is clearly a disadvantage. A global parameter-matching algorithm computes descriptive parameters for the shapes to be aligned. The most commonly computed parameters are the centroid and principal axes. Knowledge of these two

parameters determines the displacement and rotation necessary to bring two shapes into congruence. As centroid and principal axes are only determined by the *positions* of points within a shape, a system using such an algorithm must be impenetrable to nonpositional information. Like Cheng's rats, global parameter-matching algorithms return as many solutions as there are axes of symmetry. However, this type of model has the same problem as that of O'Keefe (1990; see below): the points used in calculating these global parameters must be consistent over time. Where the environment does not sufficiently restrict possible choices, they must be stored in memory. Then they must either be identified on some basis other than the global parameters that are computed from their positions, or else an iterative procedure must be used.

The evolutionary argument for using only shape is most graphically put by considering the problems confronting foodstorers such as Clarke's nutcracker. During autumn this bird hides seeds in up to 33000 caches (Vander Wall and Balda 1977, 1981), of which it has to recover at least 2500 to 3000 in order to survive and breed (Balda and Turek 1984). Between the times of storage and retrieval much vegetation will disappear or be covered by snow. Surface features will change while the large scale shape of the environment is much more likely to remain unaltered. Even animals with no need to remember specific places over long intervals will benefit from building a permanent representation of space using invariant properties of the environment. If surface features were considered, this would introduce another computational consideration. How much weight should be given to, for example, a change of odour compared to a change of colour? If all factors to be weighted are of the same kind, in this case geometrical, this problem is vastly simplified. In addition to Gallistel's arguments, many features, for example a species of plant or a particular ground texture, are likely to occur repeatedly throughout an animal's home range.

This series of experiments only shows that geometry is important for determining orientation. It has not been shown that the same principle would apply to the determination of location. It was also the shape of a single object that was so influential in determining orientation. Would shape alone have as much significance if it had to be reconstructed from the positions of discrete objects in an array or if orientation was known and location had to be determined?

Poucet et al. (1986) studied the exploratory behaviour of hamsters when confronted with an array of familiar objects. The subjects first had 15 minutes familiarisation with the apparatus, a circular open field with white walls and

surrounded by white curtains. During a 10 minutes interval a striped pattern was put on the wall and four different objects were arranged in a square array. Then the hamsters were put back for the first exploration session. The configuration of landmarks remained the same for all animals in the second session. In the third session the control group carried on with the original array (Figure 2.10). The first and second experimental groups experienced a displacement of one landmark. In the first experimental condition the displacement destroyed even topological relations. The second displacement preserved topological relations. The third manipulation was a diagonal transposition. Taking only the square array of landmarks into account this is equivalent to a reflection, preserving all properties of Euclidean geometry. If the striped pattern is considered part of the array then the transposition destroys even topological relations. As a measure of exploration, the number and accumulated time of contacts with each of the objects was recorded.

Exploratory activity decreased significantly in all groups from session 1 to session 2. It was reinstated in the third session in all experimental groups, but not in the control group. Only the first experimental group showed a significant increase in exploratory behaviour directed at non-displaced objects. In the other two experimental groups exploration was directed only at displaced landmarks. Displaced objects were always explored more than non-displaced objects.

The hamsters reacted to changes of only the spatial location of stimuli with renewed exploration, supporting the hypothesis that exploration serves to familiarise subjects not only with the features of objects, but also with their spatial relations. Experimental group 1 treated the altered array as a new situation, investigating all landmarks again. It is not clear from the data whether this is due to merely to a quantitative difference (the displacement in group 1 was larger than in groups 2 and 3) or whether it was due to the specific spatial relations that were affected. Group 1 encountered an array in which even topological relations were changed. They remained unchanged in groups 2 and 3, at least if the array of landmarks is considered in isolation. Group 2 reacted to the same transformation that made no difference to Cartwright and Collett's (1983) honey bees in a preference test. Group 3 selectively explored the exchanged landmarks in a transposition ignored by the rats of Cheng (1986). Any of the following factors might account for that difference: (1) The hamsters did not need to establish their orientation with respect to the four objects because they were not disoriented and the striped pattern could be an effective polarising cue. The diagonal transposition changed spatial relations relative to the

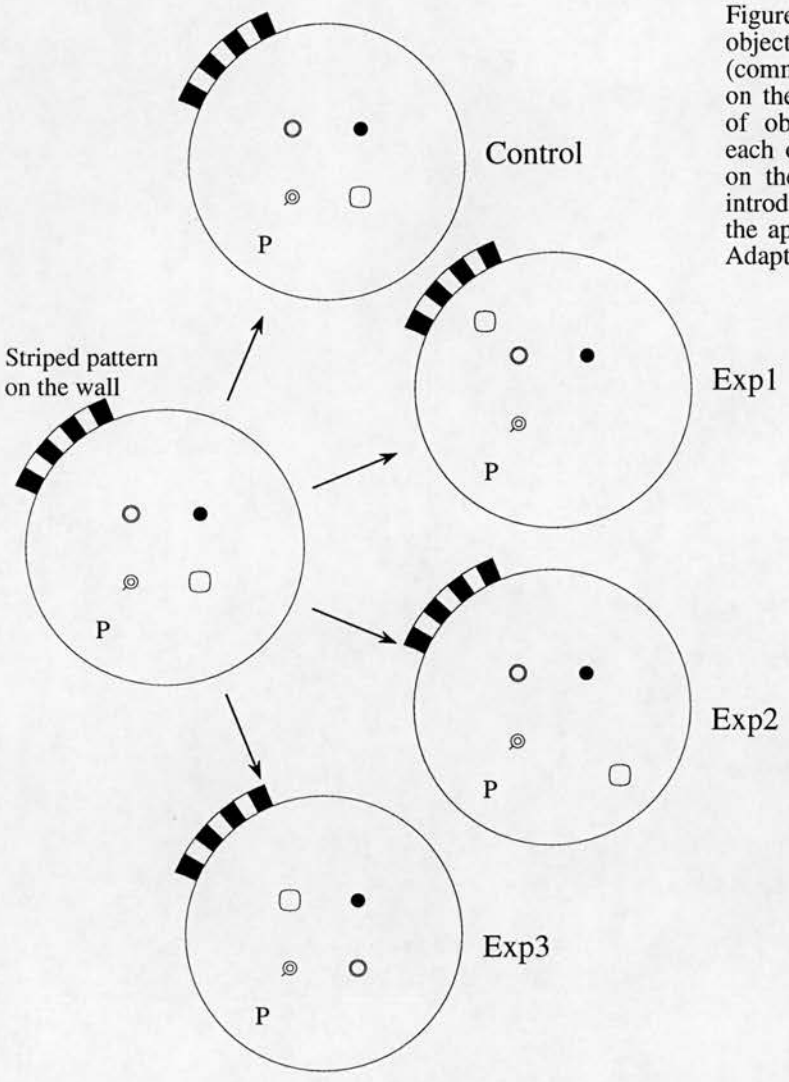



Figure 2.10. The configuration of objects during sessions 1 and 2 (common to each group) is shown on the left side; the configuration of objects during session 3 for each of the four groups is shown on the right side. The place of introduction of the subjects into the apparatus is marked with a P. Adapted from Poucet et al. (1986).

hamsters' established orientation. (2) Array shape may be relatively less important when it must be determined from the positions of several discrete objects. (3) The shape of the objects is at a sufficiently large scale relative to the array to be included in computations. (4) Featural information is more important early in learning.

Thinus-Blanc et al. (1987) extended this experiment, using the same apparatus, landmarks and dishabituation paradigm. As in Poucet et al.'s study the control group experienced the same square configuration of landmarks in all three sessions (Figure 2.11). For the experimental group A all landmarks were shifted 10 cm to form a larger square than before. The transformation for group B was the same as for group 2 in Poucet et al.'s experiment: one landmark was shifted outwards along a diagonal. Groups C and D experienced movements of the same landmark along the same diagonal, but into the array. Group E was tested with the same landmark removed.

The control group habituated further. Group B increased exploration of the

displaced, but not the non-displaced, object, replicating the results of Poucet et al. (1986). Only in group B, where the movement of a single object expanded the array, was selective re-exploration of the displaced object found. In both groups C and D, where the object moved towards the centre of the array, exploration was non-selective. In Group E removal of a landmark led to exploration not only of the remaining objects, but also of the location of the missing one. This indicates that the hamsters were able to reconstruct the configuration from partial information.

The expansion of the array of landmarks in group A, moving all four objects as far as the single object in B, did not trigger exploration. A reversal of that sequence, from large to small array in group F, gave the same result: no exploration of the altered array. As long as shape is maintained, the hamster did not react to alterations in array size.

To establish whether the configuration was encoded irrespective of the nature of its constituent elements, or whether the differential characteristics of the objects play a role in the detection of the transformations, another pair of groups replicated the array transformation of Exp B with identical landmarks. There was less exploration in these groups. While exploration of the displaced object did increase in the Experimental group, G, both compared to session 2 and compared to the Control, the change was significantly smaller than the reaction of group B to the same displacement. It seems likely that the lesser extent of reexploration in the test session is due to less exploration, and therefore less habituation, in the more homogeneous environment. In this respect, the properties of landmarks seem more important than indicated by Cheng and Gallistel's (1984) and Cheng's (1986) experiments.

Considering the experiments both of Poucet et al. (1986) and Thinus-Blanc et al. (1987) a pattern becomes apparent. Though these authors did not use Cheng and Gallistel's (1984) classification of geometrical properties it seems too useful to ignore. First, the animals reacted only to changes of spatial relations within the array of objects, ignoring the walls of the arena, the curtains and the striped pattern on the walls. Second, the only changes that did not lead to a renewal of exploration preserved the shape of the array of objects, i.e. angles and ratios of distances between objects (in groups A and F). Third, manipulations that either destroyed even topological relations, or introduced an object into the area of the original array and changed the shape, led to non-selective exploration of all objects (groups 1, C, D and E). Fourth, displacements that altered sense, or all geometrical relations between objects except topological ones, led to selective exploration of the displaced object or

objects, if the manipulation did not introduce objects into the area within the original array (groups 2, 3, B and G).

This last condition may indicate that the space within an array of landmarks has a special psychological status. According to this hypothesis the hamsters would represent the shape of the array not only by the spatial relations between the landmarks, but also as an empty area. If a single object is moved out of this area, spatial relations between the remaining objects and the shape of the empty area are unaffected. This is treated as an altered, but recognisable situation. If a landmark is moved into the area that should be empty, the shape of the area now enclosed by the new landmark array does not fit memory. The configuration is treated as completely novel. This hypothesis is especially interesting because of a problem Worden encountered when implementing his fragment fitting theory (1992) in a computer model. He found that he had to include representations of empty areas to limit the number of fragments the system tried to

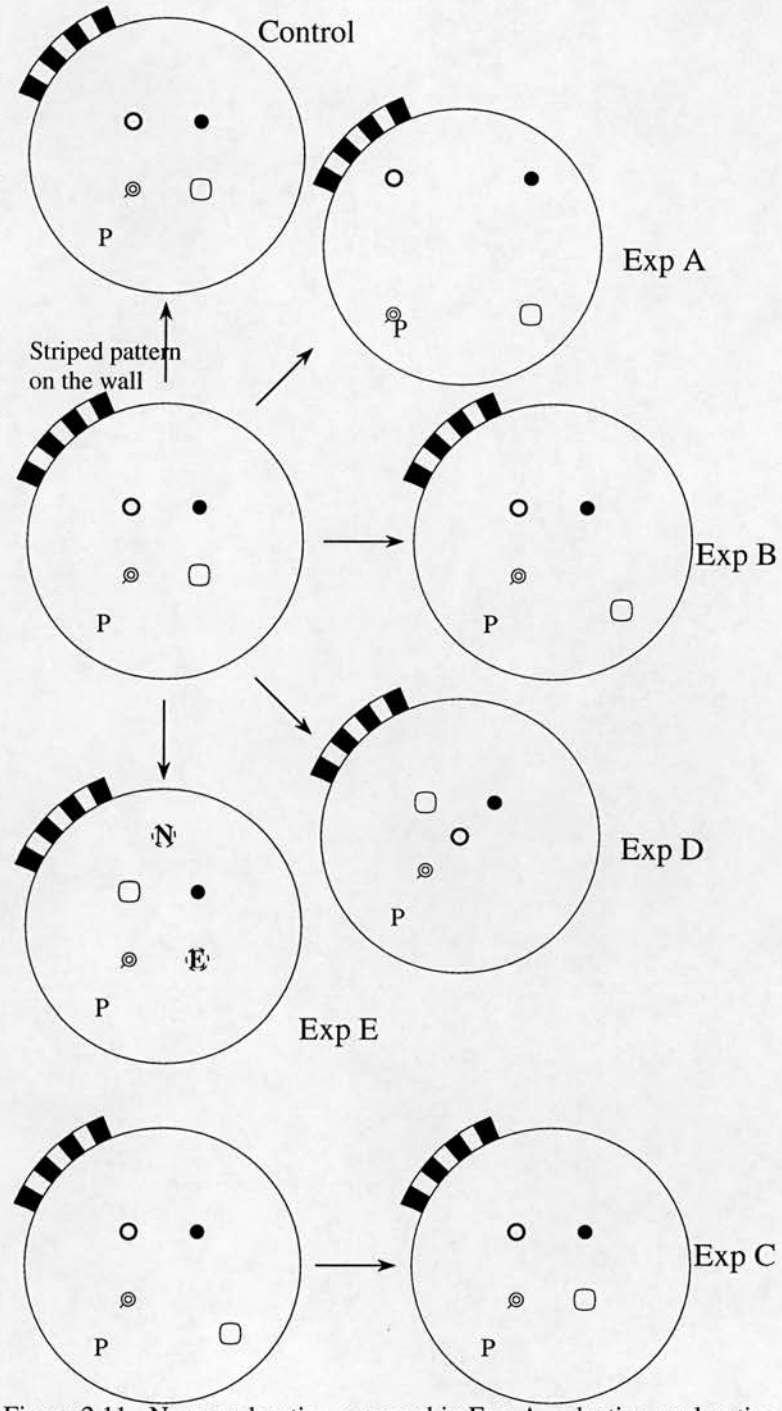



Figure 2.11. No reexploration occurred in Exp A, selective exploration only in Exp B, exploration of all landmarks in Exp D and C. Deletion of a landmark in Exp E led to exploration of the empty spot E when compared to another neutral area of the same size, N.

create to fit the available data (Worden, pers. comm.).

All the interpretations advanced above are based on the assumption that the subjects' representation of space is allocentric. As the animals were always introduced into the apparatus at the same point, whether exploration might have been triggered by a mismatch in the view from the starting point. However, this does not explain the lack of reexploration in groups A, C and F. The changes in the configurations of their arrays should have been visible from the starting point. The assumption of allocentric representation is probably correct.

Tomlinson and Johnston (1991) used a similar dishabituation procedure to study hamster's knowledge about the spatial location of olfactory cues. Two objects were placed 25 cm apart in a circular arena. They were identical except for the odour cue they carried. The control group was exposed to the same arrangement of odours in all three sessions. For the experimental group the odours swapped places in the last session. In the first experiment the animals were always introduced into the arena at the same location. The only procedural difference in the second experiment was introduction of the animals at the opposite side of the arena, so that an egocentric representation would trigger a change in the control, but not the experimental group.

In both experiments the control groups continued to habituate in the third session, while exploration increased significantly in the experimental groups. The results show not only that hamsters acquire knowledge about the location of olfactory cues, but also that this knowledge is contained in an allocentric representation.

## 2.5. Mapping - Integrating landmark information

The next step in the integration of landmark information is to build a unitary, internally consistent representation. O'Keefe and Nadel's (1978) characterisation of cognitive mapping has for many years been the most influential one. Primarily intended as a theory of hippocampal function, it has some weaknesses as a theory of navigation. O'Keefe and Nadel's derivation of the properties of cognitive maps relies strongly on analogy with physical maps and contrasting their properties with those of routes.

Routes are goal-centered and not necessarily reversible. From a point A one may be able to reach B simply by heading towards a conspicuous landmark located there. While in this way B can be approached from any direction only one direction leads back to point A. For a different example, to reach a cottage somewhere on a hill one may start walking along an inconspicuous forest path until reaching an open valley, turn and follow a stream until the cottage is in sight. When returning one may easily

miss the entrance to the path. Routes are also inflexible. If a landmark has been missed, was not recognised or has disappeared, the remaining information may be useless. Only landmarks that can guide either directly to the goal or back to some point on the route make it still possible to reach the goal.

Maps are relatively invulnerable to loss of information, are flexible, require knowledge of the strategies used to encode spatial information and are slower. They allow planning of novel routes, including shortcuts and detours. They are said to be efficient storage devices that contain a great deal of information without redundancy. As outlined above, explicit representation of distances between locations leads to combinatorial explosion if all possible relationships are included. This implies that if efficiency of storage is to be a characteristic feature of a map, then it must rely on implicit storage of spatial relations. However, in that case all spatial relations must be recovered from the map by a readout mechanism. In order to determine the cost of an excursions in terms of time or energy, this mechanism must look up at least distances between points, possibly also the type of terrain and how easy it is to traverse, whether a detour is necessary, and what detour would be most appropriate. That means that most of the interesting features of the system would be not in the representation, but in the process that reads out that information. This point tends to be overlooked, because map reading appears to be so easy and natural when using a physical map that we tend not to notice it. O'Keefe and Nadel provide no characterisation of map reading in computational terms. They only offer some hypotheses regarding the physiological implementation. This is acceptable in a theory of hippocampal function, which O'Keefe and Nadel intended to propose, but is a major weakness in a psychological theory of navigational competence. When trying to derive predictions from this theory, it is necessary to consider whether a feature of interest is a property of the representation, the method of data acquisition, or the readout mechanism.

O'Keefe (1990) developed a more detailed model of cognitive mapping. Locations are assumed to be represented by reference to an origin and reference direction for vectors with polar coordinates. The model does specify a readout mechanism that can provide the displacement vector to a goal. The origin of the coordinate system is the centroid, defined as "*the geometric centre or centre of mass of the cues in the environment*" (O'Keefe 1990, p. 306). It is calculated by taking the grand mean vector of the cue vectors. The reference direction is the eccentricity, determined by averaging the slopes of all possible lines between pairs of landmarks

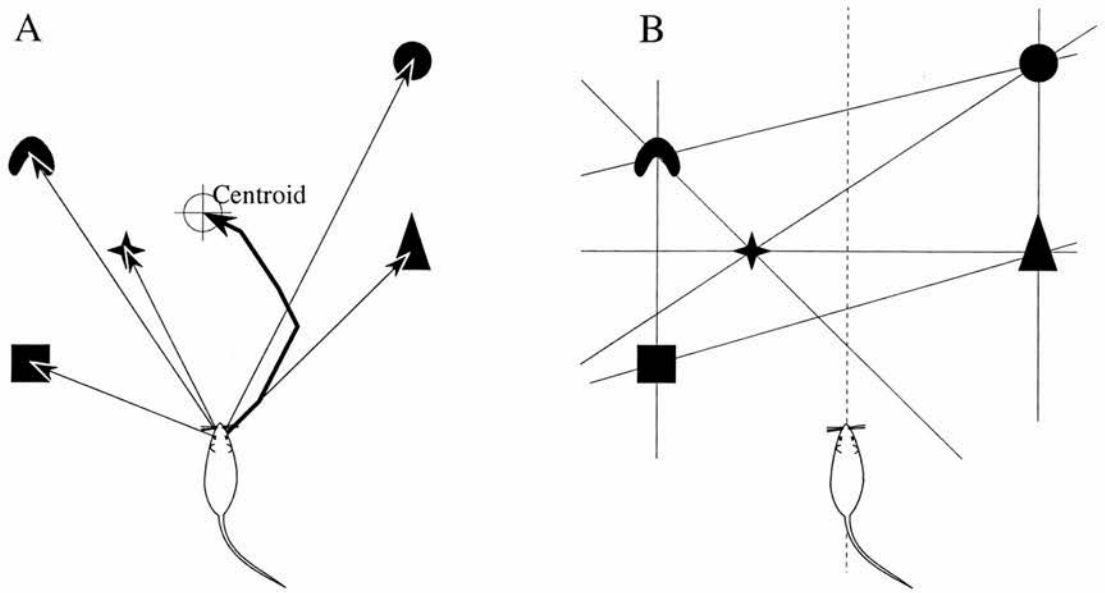



Figure 2.12. O'Keefe's centroid model. a) The centroid is the grand mean vector of all egocentric self-landmark vectors. It is invariant as long as the component vectors point to a consistent set of landmarks. b) The eccentricity is the average of slopes $\Delta Y/\Delta X$. If the egocentric axis becomes parallel to a line between two landmarks, $\Delta Y$ approaches zero and the slope approaches infinity. As defined the eccentricity is not invariant. A principal axis would be.

(Figure 2.12). The slope of the lines is defined as $\Delta Y/\Delta X$ where the y-axis is the polar axis of egocentric space. Whenever the line between a pair of cues is approximately parallel to this axis, $\Delta X$ approaches 0 and the slope approaches infinity. As the eccentricity is the average slope of all these lines it will also approach infinity and will be parallel to the polar axis of egocentric space whenever a line through any arbitrary pair of landmarks is parallel to this axis. The eccentricity is not invariant with rotation and therefore has little value as a reference direction in an allocentric representation. I will therefore assume that instead it is equivalent to the principal axis of an array of landmarks. It is not clear to me how the polarity of the resulting line would be computed. The choice may be arbitrary.

The original theory of O'Keefe and Nadel (1978) emphasised the resistance of the locale system to loss of information. The proposed model of O'Keefe (1990) is not resistant to such loss of information if coordinates are assumed *always* to be determined in relation to centroid and eccentricity, because both centroid and eccentricity would systematically shift if landmarks were removed. Landmarks farthest from the centroid would have the greatest effect. Consider the landmark array in figure 2.13. Removal of the landmark at the apex of the triangle will change the eccentricity by 90° and will move the centroid farther than removal of either landmark at the base. A vector from the centroid to a goal should be displaced and rotated by equal amounts. This sensitivity to distal landmarks cannot be reduced by

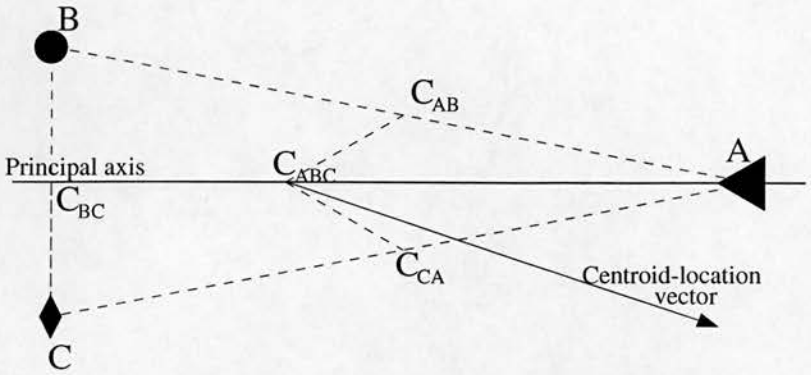



Figure 2.13a (above). Array of three landmarks, A, B, and C. $C_{ABC}$ = centroid of landmarks A, B, and C; $C_{AB}$ = centroid of landmarks A and B; $C_{BC}$ = centroid of landmarks B and C; $C_{CA}$ = centroid of landmarks C and A.

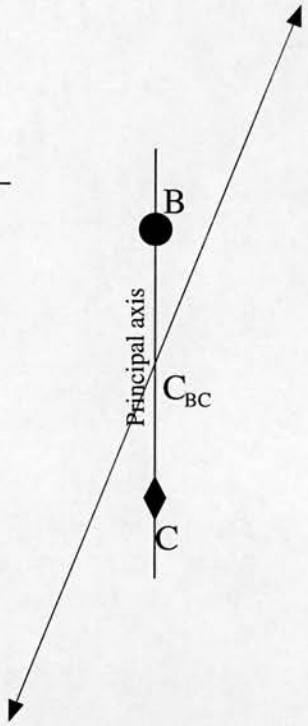



Figure 2.13b (right). Removal of landmark A moves the centroid midway between B and C and rotates the principal axis or eccentricity by + or - 90°. The centroid-location vector is displaced and rotated accordingly. Whether this rotation would be clockwise or anticlockwise is not determined by the model.

giving them lower weights. Weighting landmarks according to their distance from the animal would make centroid and eccentricity dependent on the animal's location. Weighting landmarks according to their distance from the centroid would necessitate an iterative procedure, significantly adding to the processing demands.

Another problems becomes apparent when taking into account the influence of measurement errors. Consider the arrangement of landmarks and goal in figure 2.13a. A subject tries to return to a location far from the centroid but close to a landmark. Even if the location of the centroid has been determined without error, it is likely to have a larger error than a vector from landmark A, at a smaller distance (Weber's law, as observed by Cheng, 1990). Therefore this landmark should be given more weight, but this is not possible because the model only allows the definition of a location with respect to the centroid and the eccentricity. This problem could be avoided if the animal determines its location by reference to the closest landmarks, and uses knowledge of their coordinates to determine its own global coordinate. In that case the location of the origin of the coordinate system can be arbitrary. There would be no reason for calculating the centroid.

Most of the problems of the model originate in the insistence on the representation of locations by exclusive reference to a global coordinate system. Clearly, the model requires at least an extension so that it can use multiple frames of reference for separate groups of landmarks.

In another paper O'Keefe (1991) appears to make a move toward such an extension. He attributes the calculation of the centroid to hippocampal CA3 cells, "*each of which makes an estimate of the centroid on the basis of the limited subset of cues available to it. These minicentroids form a matrix that uniquely identifies each place in every environment*" (p. 232). Knowledge of the location of some minicentroids may allow the determination of the location of other minicentroids or the overall centroid, perhaps by a process of pattern completion rather than averaging minicentroids. There are two preconditions. First, the subsets of cues must be consistent, else there can be no consistent matrix of minicentroids. Second, it must be possible to specify a location without reference to the overall centroid. In this case the overall centroid becomes again redundant and the model becomes similar to Worden's (1992) fragment fitting model. In summary, the eccentricity as defined by O'Keefe (1990) is not invariant with rotation and cannot provide an allocentric reference. The centroid is redundant because location of the origin of the coordinate system is arbitrary. The two main parameters of this model do not fulfil their intended functions.

The central feature of Worden's (1992) fragment fitting model is the existence of multiple frames of reference, though derived from considerations of computational efficiency. Navigation requires the storage of a large amount of information and its rapid processing. If processing capacity were distributed amongst the memory storage, for example a topographic mapping of the environment to the surface of the cortex or hippocampus, with an active area of processing around the current location, only a small area would be active at any one time. This would waste much processing capacity, in contrast to, for example, retinotopic maps whose whole area is used. Worden proposes that processing would be separated from the long-term memory, loading into a short-term memory only currently relevant information. Selection of what is relevant requires breaking up information into smaller portions. A compromise must be made between very fine divisions, making many decisions necessary regarding what is relevant, and creating big chunks of information, where at least portions of any one chunk are likely to be irrelevant. Worden suggests that "*fragments of terrain data ... may refer to large or small areas of terrain; but whether large or small, a fragment gives information about only a small number of objects in the terrain.*" As the selection process here matches consistent sets of landmarks in long term memory to the perceived environment, the problems of 'Keefe's centroid model are avoided. Worden also does not attempt to fix the origin of a global

coordinate system. The term "fragment" is synonymous to other's "reference frame".

As the information content of each individual fragment is relatively small there must be a large number of them to cover all of an animal's navigable range. This, in turn, necessitates an effective retrieval mechanism which is assumed to be associative. The retrieval mechanism could select fragments containing features matching those currently perceptible, or fragments containing a goal location. Whether large- or small-scale fragments are chosen would depend on the range and accuracy of navigation required. Knowledge which fragments are relevant and perhaps even in which fragment the animal is located is not in itself sufficient. The navigational processor must also determine position within fragments and assemble fragments into a larger map. The assembly of a map is assumed to proceed in parallel, in a number of loosely-coupled fragment fitters, each trying to optimise the fit of one fragment at a time into the overall model.

Finally, this leaves the problem of how to allocate multiple fragments to multiple fitters without duplication or assigning fragments relevant to the same area to the same fitter, which could retrieve only one of them. Fragment fitters also create new fragments when necessary. If this takes place only in a fitter left unoccupied after all relevant fragments have been loaded in, this should only happen if that fitter's memory contains no relevant fragment. If there is no fitter free, available information should suffice to solve the problem. For that scheme to work the fitters need good criteria for what information is relevant.

For the purpose of local navigation within a fragment the animal stores in short-term memory two-dimensional vectors representing the positions of nearby objects and its own position. Worden advocates position vectors from the origins of unique allocentric coordinate system in each fragment, on the grounds that an egocentric representation would require parallel updating of all subject-landmark vectors. This could lead to different errors accumulating in each vector, thereby degrading the quality of the map. This should not be a big problem. If a fragment covers a small area the animal will not have much opportunity to accumulate errors before entering a freshly fitted fragment. Also, the computational demands of direct landmark-subject vectors are less than those of a single vector in a coordinate system. Before the single vector can be used, the origin of the coordinate system must be determined by reference to the egocentric positions of landmarks, adding one computational step.

Each fragment contains the following types of information: (1) the geometric relations between objects, (2) non-geometric properties of each of the objects or

places, (3) the bearings and other properties of visual cues visible from each of the objects. A fragment can be retrieved because one of the objects forming its vertices is matched, on the basis of its non-geometric properties, to an object already in the map. The new fragment is displaced until the vertices containing the same object are in congruence. It is rotated until the bearings of another object are the same in both fragments. If the fragments have more than one object in common the new fragment can be rotated until those objects are congruent. If this is not possible the fit can be rejected. Computer simulations showed that these criteria did not always sufficiently constrain the fitting process. If only some vertices matched a fragment already in the map, then the remaining non-matching vertices would be treated as additions to the map, predicting the presence and locations of new objects. The addition of information about empty spaces allows the rejection of a fit that predicts the presence of objects in places known to be unoccupied. Studies by Poucet et al. (1986) and Thinus-Blanc et al. (1987) have shown that comparing the extent of empty areas to previous experience may be a factor in deciding whether an environment is new or familiar.

A variation on the fragment fitting process allows efficient retrieval of relevant information when planning a route to a distant destination. Obvious criteria for the selection of two fragments are the objects in the fragments that contain the goal and the current position. Unless these two fragments have a common border the problem arises how to select the intervening fragments. One possibility is to add on fragments such that patches of fragments grow around current position and goal until a fragment is found that joins the patches. The number of fragments selected by this process would be proportional to the square of the ratio of the distance to the goal and the average diameter of the fragments. Therefore a distant goal will favour retrieval of large scale fragments. However, they may not provide sufficiently detailed information to choose a route. Alternatively, fragments might overlap. Then large scale fragments can contain small scale fragments, an interpretation consistent with the results of Margules and Gallistel (1988), Etienne et al. (1990) and Dallal and Meck (1990, see discussion below). Goal and current position would be connected by large scale fragments. The retrieval of small scale fragments could then be limited to those contained in selected large scale fragments.

Both these models share the problems caused by insistence on a coordinate system, O'Keefe's model to a greater extent, because it is largely a model of how the origin of the coordinate system is determined. The question arises whether it is

possible to represent location without use of a coordinate system. The basic principle of using a coordinate system in, say, a two dimensional space is to decompose location into two components. In a polar coordinate system these are distance from the origin and angle to a reference direction, in a Cartesian one two distances along non-parallel directions. Its analog in using a physical map would be the specification of location by the number pair of a grid reference. There is an alternative. On a physical map one can specify a location by marking it, perhaps with a pen or by putting down a token. Determination of spatial relations to other locations on the map would still require a ruler and knowledge of scale, but is possible without using a grid reference. In fact, many maps do not have a grid. Such direct analog modelling, rather than decomposition of components, is also known in biological systems. For example, the auditory system of the barn owl computes azimuth from binaural sound delays and elevation from intensity differences. Then these two components, rather than used directly as coordinates, are unified in a two-dimensional map in which sound direction is marked by the location of a patch of neural activity (Knudsen et al, 1987). The firing of hippocampal place fields can be interpreted in the same way, as a travelling patch of activity, giving an analogue coding of position in the environment. There is no topographic coding in the rat hippocampus as there is in the inferior colliculus of the barn owl. I will attempt to show, in appendix A, that this improves efficiency. In the meantime, for simplicity and easier visualisation, it will be assumed that there is topographic mapping of location of place fields onto locations of place cells. This analogue representation without use of coordinates is a shared feature of several models of spatial representation in the hippocampus.

Burgess et al. (1994) and Burgess and O'Keefe (1995) assume that place fields are generated by the combination of input from cells with tuning curves responsive to distance from a landmark (Figure 2.14). As a rat moves about an environment, its place cells compete for sensory information. Normally, each cell ends up firing at specific distances from two landmarks (though input from three or four landmarks would prevent the multiple peaks that are possible with only two landmarks). Once each cell that is to be used has a place field, the learning stage is over as far as the map is concerned. In a new environment place cells can be recruited at random for a new representation. Although this competitive learning establishes a link between a pair of landmarks at specific distances, it differs from conventional associative learning in one important respect: The learning rule does not detect a correlation. It

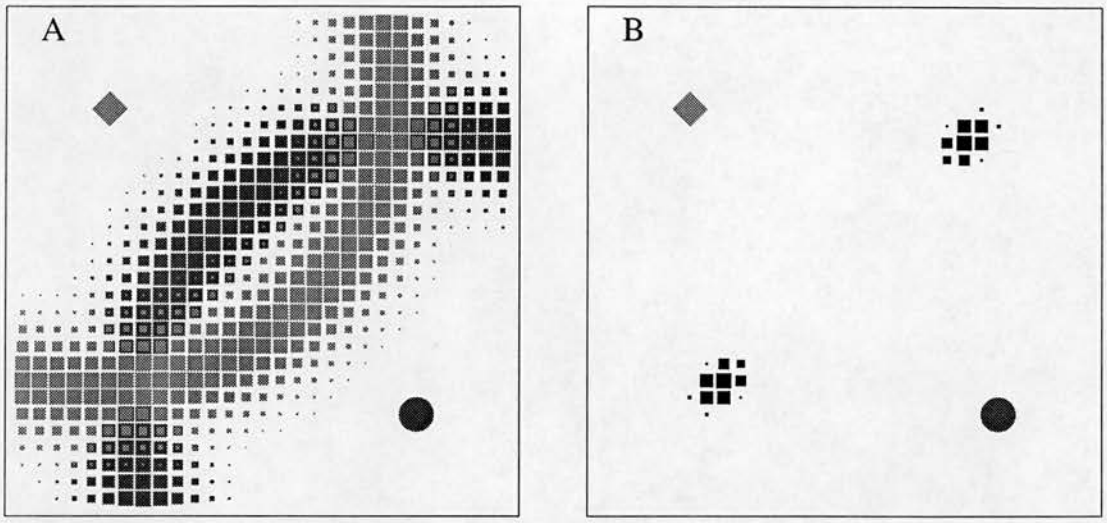



Figure 2.14. Place fields in Burgess et al's (1994) model. (A) Each hippocampal place cell receives input from two cells, each sensitive to distance from a specific landmark. Their receptive fields are annuli round their respective landmarks. (B) The place field results from adding these inputs and applying a threshold function that retains only the top 20%. In this example there are two intersections of the distance-sensitive fields in the environment, resulting in a place field with a double peak. The ambiguity could be resolved by either selecting landmarks that produce the second peak outside the boundaries of the environment, or by adding directional information or input from a third distance-sensitive cell.

does not need to predict place cell firing based on landmark distances, because which precise place cell is assigned to a pair of landmarks is a completely arbitrary choice. All that matters is that *one* cell does get assigned, and quickly. Which cell wins is determined by the weights randomly assigned prior to any input. The determination of place cell firing exclusively by pairs or subsets of landmarks has an experimentally testable consequence. If the landmarks driving a particular place cell are moved, the place field will move with them. Cells driven by non-overlapping sets of landmarks will be completely unaffected. Those driven by some shifted and some other landmarks will change their place fields in predictable ways. There should be no systematic spatial relationship between the place fields that are influenced by a landmark shift and those that are not.

The pattern of place cell firing can only provide information about present location. The model includes a readout mechanism which, at the present stage of development, consists of goal cells with firing fields large enough to cover the whole environment. If there were a single cell, it would only be possible to determine distance to the goal from the firing rate. A possible solution is to have a group of cells whose fields surround the goal. The sum of their firing rates will specify distance, their relative firing rates direction. If the goal cell with a field to the south fires strongest, then the rat must be south of the goal (Figure 2.15). The fields of the goal cells are placed appropriately through phase coding. Only in the middle of the

theta rhythm is there maximal firing of the place cell whose field coincides with the rat's position. In the early phase cells fire with fields behind the rat, in the late phase cells with fields in front of the rat. If learning of goal fields occurs only in the late phase of the theta rhythm, and if the rat turns in various directions once it has reached a goal, fields in several directions will be built up. The goal fields must be large enough to cover the whole environment, because their information is only accessible within their fields. In order to achieve that there must be either an intermediate stage where input from many place cells converges to create large fields (Burgess et al., 1994), or the model must make use of the different scales of representation available in the hippocampus (Burgess and O'Keefe, 1995), with cells in the ventral region having larger fields than those in the dorsal region (Jung et al., 1994). In the latter case there could be separate sets of goal cells, some with relatively small goal fields for accurate short range navigation, and others with larger fields for displacements over longer distances. Alternatively, if place fields of all sizes feed into a goal field, its shape will be asymmetric with a steep slope on the side near the goal and a shallow slope on the other side. In all cases, each goal receives its own set of goal cells, all utilising the same map.

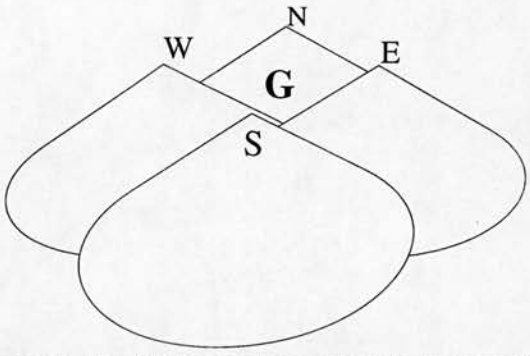



Figure 2.15. At the goal the rat looks in several directions and connects either directly the place cells, or intermediate cells with a large place field, which lie ahead of it, i.e. those firing late in the theta cycle, to goal cells. The sum of firing of all the goal cells provides a measure of distance to the goal, their population vector specifies the direction.

In this model there are up to two learning steps. First, the assignments of two landmark fields to each place cell, creating their place fields. Second, the assignment of place cells to goal cells. Place cell firing is entirely driven by landmarks. Dead reckoning has, at present, no place in this model. The fields of distance-sensitive cells are taken as given. There is no learning of these fields. The map is homogeneous, with no special location serving as the origin of a coordinate system. The activity peaks travels on a two-dimensional surface, rather than being decomposed into two one-dimensional variables. Only goal locations could be considered as origins of coordinate systems, the coordinates specified by the relative and aggregate firing rates of the goal cells. Coordinate systems are not necessary to create a spatial representation.

A feature of the readout mechanism, rather than the map, is that multiplication of

distances by sine or cosine of an angle is not necessary. Once a set of goal cells is established, anchored to landmarks only through the place cells, distance to the goal is only specified through the goal cells. Addition of self-landmark and landmark-goal vectors is not needed. The procedure is analogous to marking a goal on a physical map, determining its location relative to landmarks only when that mark is made, and subsequently only laying a ruler onto the map from the current location to the goal.

The readout mechanism, as specified at present, has several limitation. It is not possible by use of the goal cells alone to determine distances between multiple goals. The relevant information is present in the output, but the necessary computation would be vector additions, which would need to be performed on the output from the goal cells. It is not possible to read out the location and extent of obstacles from this map, unless that information is linked to other goal cells, which may have repellent rather than attracting properties. In effect, the only information contained in the map itself is the position of place fields in the environment. All information about what is at such a location must be bound to goal cells. Although the map itself is homogeneous, the information provided by goal cells may not be. That learning may concentrate on the most important areas, minimising demands on processing and storage. In this model O'Keefe and Nadel's (1978) prediction that the construction of a map is not goal driven, and that all available information is incorporated, could apply only to the locations represented in the map, not to the information bound to the goal cells.

Despite its apparent limitations, this model offers several advantages over the representations discussed above. First, it makes efficient use of information about distance from landmarks. Each landmark-distance tuned firing field is used in the specification of several place fields, each time in combination with a different second landmark-distance field. Second, once the map is established, places can be quickly linked to goal cells. Third, the number of goal cells required grows only linearly with the number of places they cover, rather than quadratically. These uses of the map are possible by having additional readout mechanisms downstream from the goal cells.

A possibly more fundamental problem is that a goal can only be established once the animal has arrived at the goal location. It is not possible to specify a goal remotely, as in open loop walking or in Cramer's (1995) experiment, where monkeys watched grapes being hidden in a familiar enclosure. Spiders have also shown to be capable of determining a goal from a distance, then following a path to that place without being able to see the goal object (Hill, 1979). Likewise, toads plan a route to

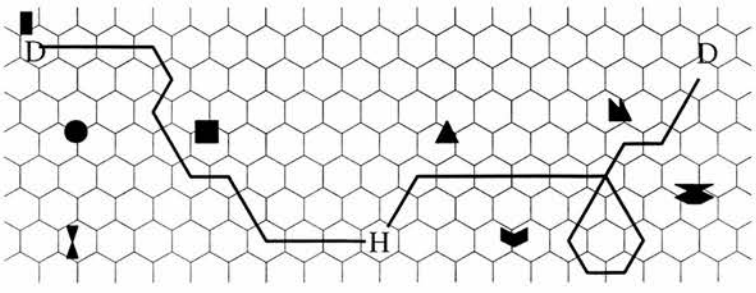
distant prey and execute at least a segment without further visual feedback (Lock and Collett, 1979; Collett, 1982). However, in both spiders and toads this capacity may not depend on familiarity with the environment. Though there was repeated testing no data are shown indicating an improvement over time or a necessity for familiarity. The timecourse over which this remote localisation of a goal occurs is in the order of seconds. However, Bednekoff and Balda (1996) have found that some corvids can recover seeds they observed being cached two days earlier.

A model proposed by McNaughton et al. (1996) uses essentially the same kind of map, but assumes that place fields are primarily driven by dead reckoning and only secondarily by landmarks. This apparently minor change of emphasis has some important implications for the organisation, integration and acquisition of information, and will therefore be discussed in chapter 3.

Brown and Sharp (1995) also proposed a model using a place cell map. The map is derived from 'local view' input, with non-overlapping place fields. As in the models discussed above, if size and density of place fields are, on average, uniform, the map contains all information needed to read out distances and angles between locations. However, the readout mechanism, based on stimulus-response associations, is not able to access that information. Brown and Sharp assume that while travelling to a destination rats associate each combination of place and orientation, defined by the firing of a single hippocampal place cell, with a right or left turn. Then the rat moves until hitting the next familiar place and turns according to the association it retrieves there (Figure 2.16). There is no distance component to the response; it is "ballistic". If the model rat made an error and failed to hit a place that has a response associated with it, it would just keep going or would have to respond at random.

In order to learn a path to a goal, the model rat must first find it through random search. Then the most recent responses are strengthened. This ensures that when

Figure 2.16. "Ballistic"stimulus-response associations when there is a high density of familiar places. Each place, defined by the firing of a hippocampal place cell, is shown by a hexagon. For simplicity, and following Brown and Sharp, these are assumed to be non-overlapping, though that is only a feature of their specific model and not necessary for all possible ballistic S-R models. The diagram shows landmarks, a home location, two paths and two destinations. On arrival at a destination the responses made on the outward path are stamped in, giving more weight to more recent responses. As there can be only one response at each place. the learning algorithm will remove loops, as in the path on the right.



there have been several responses where the search path crossed in one place, only the response which leads on to the shortest following path segment is reinforced.

The neural implementation of the model assumes that hippocampal place cells are connected through inhibitory interneurons to two sets of motor units (Figure 2.17). Activity of a unit in one set turns the animal left, in the other set right. There are two motor units for each hippocampal cell. Activity in one place cell inhibits, through the interneurons, activity in all but two motor units, specific to that place cell. These connections are all assumed to have fixed weights, although in practice learning will be needed to assign to a place cell the corresponding set of 'local view' cells. Left turn and right turn motor units are mutually inhibitory, so only one will fire. Which one does is determined by adjustable input from head direction cells. When arriving at the goal a competitive learning rule strengthens all connections that were recently active and weakens all others. A short time horizon for this learning would limit the spatial range of learning. A long horizon risks stamping in circuitous approaches, as responses made long ago were probably wrong and led to detours. Having been active, the connections would nevertheless be strengthened. The problem is solved by raising the activity trace of all inactive connections by a constant amount. All connections having a smaller activity trace, i.e. those that were active long ago, are then weakened. The need to have a separate motor unit for each place cell arises from the egocentric coding of the response. If response were defined as a geocentric direction, each place cell could connect to a common set of motor units. But as the model only keeps track of which egocentric responses were performed, not of their sequence, the responses must be kept separate and assigned to specific place cells by using separate motor units.

The model allows some degree of generalisation. The authors distinguish

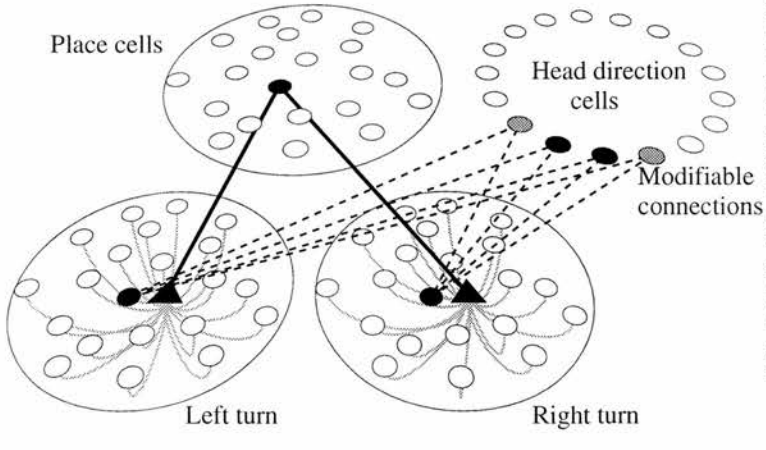



Figure 2.17. Each place cell connects to two inhibitory interneurons. Here only the connection from the currently active place cell (black circle) to the corresponding interneurons (black triangles) are shown. Each interneuron inhibits all but one motor unit in a set of right turn or left turn units (grey lines). Motor units receive modifiable inputs from all head direction cells. Here only inputs between active head direction and motor cells are shown (dashed lines). Mutually inhibitory connections between populations of left turn and right turn units ar not shown. Adapted from Brown and Sharp (1995).

between directional and spatial generalisation. Directional generalisation is knowing whether to turn right or left in a familiar location when facing a novel direction. This is possible because head direction cells are broadly tuned and four are active at any one time. If a novel direction is sufficiently similar to the previously experienced one that the learned response is appropriate, then it is likely that they will have overlapping populations of active place cells. Inactive connections are weakened, so if the model faces a direction without any overlapping head direction activity, the non-adjusted connection to the other turn unit are likely to be stronger and the model will turn in the opposite direction. This second mechanism of generalisation relies on direction being bounded. Spatial generalisation is knowing which way to turn when facing a familiar direction in a novel location not far from a familiar one. Coarse coding would allow spatial generalisation, but may introduce problems in assigning responses, as several motor units would be active at the same time. As location is not bounded, suppression of connections to inactive motor units would not produce appropriate generalisation.

In effect, this model use as stimulus a combination of place and direction, the response is a turn. The S-R mechanism is "ballistic": turn in the right direction, then keep going until hitting the next recognisable place that has a response associated with it. In principle the place cell map is not necessary. The 'local view' neurons could be connected directly to the motor units, but then the capacity for generalisation would be lost. Brown and Sharp acknowledge that the model cannot account for latent learning, as found by Keith and McVety (1988), or for place cell firing in the absence of visual input (O'Keefe and Speakman, 1987). A characteristic they do not mention is that the model has neither any need for information about distances between places, nor is able to read distances from the place cell map in any way. In contrast to the model of Burgess and coworkers, there is no way to extend the model of Brown and Sharp to chose between routes or plan an efficient route between multiple destinations.

## 2.6. Dead reckoning

Dead reckoning or path integration is the updating of position relative to a known starting point by calculating displacement through the integration of speed and direction. As errors inevitably accumulate, this requires periodic resetting to known values at some familiar reference point. Regardless of the way in which the relation between home and current location is represented, it is possible to use information derived from path integration in several ways, classifiable by increasing versatility.

1) Dead reckoning may be initiated and reset only at a home location. The system will only ever have information about the spatial relationship between home and the current location. If a coordinate system is used, home would be the origin.

2) There could be several such path integration mechanisms working in parallel and independently. An inactive path integrator may initiate dead reckoning at some point of interest, to allow return there later. Each path integrator would only be reset at its point of initiation. Errors in estimating distance and direction would be shared between the path integrators. Random errors in computation would be independent, and the location estimates of the path integrators would drift relative to each other. This strategy would also be limited in the number of locations it can keep track of.

3) There could be only a single path integrator whose output can be stored in long term memory. Reversal of a remembered vector from a destination towards home, and addition to the current home vector would provide a vector from the current position to the remembered destination. The readout mechanism would need to be capable of switching to this new vector while the path integrator keeps updating position relative to home. Because different locations are not kept track of independently, it is possible to increase the accuracy of a location estimate by averaging across several visits. This will be discussed in some more detail in chapter 3.

Path integration does not necessarily rely exclusively on internally generated information such as proprioceptive and vestibular cues and efference copies. The visual flowfield can contribute to estimation of linear and rotational speeds without relying on specific and identifiable cues. Nevertheless, some species rely on external compass cues in their estimation of orientation. There may be two reasons for that. First, Séguinot et al. (1990) showed that path integration is more sensitive to errors in the estimation of orientation than of distance. Second, compass cues such as the sun tend to be perceptible throughout the whole possible range in which an animal may need to navigate. Use of a compass therefore does not require location-dependent cues. This independence from location-specific information is one of the major advantages of path integration, allowing its use even in unfamiliar environments, during exploration or unexpected displacements.

There are three basic ways of performing path integration or an approximation of it. Jander (1957) suggested averaging direction of travel over time, making the

assumption of travel a constant speed. This method gives an accurate homing direction for all journeys with two outbound legs of equal length. For example, travelling equal distances north and east one ends up northeast of the starting point. Even in this simple example, the algorithm fails for legs of different lengths. It predicts an overall travel direction of 60° east if the eastbound leg is twice as long as the northbound leg, instead of the correct value of 63.4°. This would not matter if the results corresponded to the errors found after such two-leg journeys in several species (see Séguinot et al., 1993, and review by Maurer and Séguinot, 1995; Figure 2.18). However, Jander's algorithm does not reproduce experimentally observed homing errors.

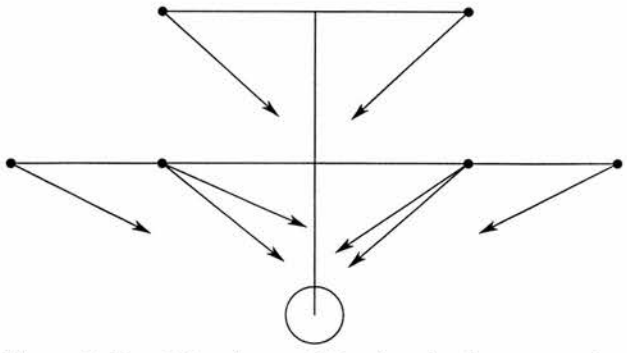


Figure 2.18. Directions of homing in hamsters after outbound journeys with legs of 1m and 2 m length in orthogonal directions (Adapted from Séguinot et al., (1993). Home is shown as a large open circle, the points where the return is initiated as smaller black circles. The hamsters systematically overestimate the turn needed to take them back. Other species show a similar bias in this situation (bees: Bisetzky, 1957; spiders: Görner, 1958; ants: Müller and Wehner, 1988; humans: Sauvé, 1989).

The next approach is to calculate position relative to the starting point. The information available to a path integration mechanism is speed or distance travelled within a finite time interval, $\Delta s$, and direction of travel relative to some compass cue or internally generated reference direction (Figure 2.19). Using a Cartesian coordinate system, $\Delta s$ and $\lambda$ are used to calculate the path components along x- and y-axes. Assuming a polar coordinate system, location is defined by the angle $\upsilon$ between the current position, the nest and the reference direction, and by the distance $r$ from the nest. The animal must compute the increment of radial distance, $\Delta r$, and the increment of the nest angle, $\Delta\upsilon$. The solutions for small increments are, assuming $\Delta q$ small compared to $r$:

| Polar coordinates | Cartesian coordinates |
|---|---|
| $\Delta r = \Delta s \cos(\lambda - \upsilon) = \Delta s \cos \delta$ | $\Delta x = \Delta s \sin \lambda$ |
| $\Delta q = \Delta s \sin(\lambda - \upsilon) = \Delta s \sin \delta$ | $\Delta y = \Delta s \cos \lambda$ |
| $\Delta\upsilon = \Delta q/r = \Delta s \sin(\lambda - \upsilon)/r = \Delta s \sin\delta/r$ | |

Mittelstaedt (1973, 1983, 1985) developed a model intended to account for the interaction between a light source serving as external compass cue, and an internally derived directional reference in spiders. The model consists of a mathematical characterisation of the required input-output function and a suggested control

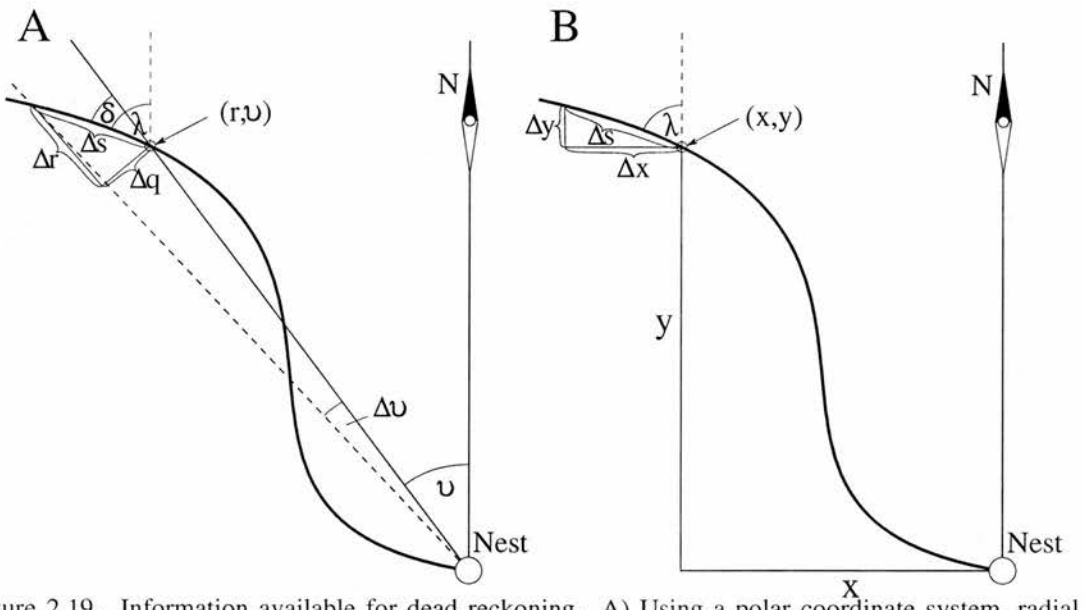



Figure 2.19. Information available for dead reckoning. A) Using a polar coordinate system, radial distance from the nest r and nest angle u relative to some reference direction describe the position (r, υ) of the ant. Locomotion in direction l by a path increment Ds results in a new position (r + Dr, υ + Dυ), as long as Ds << r. B) Using a Cartesian coordinate system the same path increment Ds and direction l are decomposed into increments Dx and Dy, added to the current position (x,y).

architecture that could implement this function. Mittelstaedt suggests that use of a Cartesian coordinate system requires fewer assumptions to implement the required coordinate transformations. He also specifies a readout mechanism that can create motor commands directly from the components of the home vector, sensory input or a remembered goal vector, without having to convert into direction and beeline distance. X and y coordinates are combined with sine and cosine of the heading to provide separate turn (right or left) and run (forwards or backwards) commands. For a given heading each of these functions divides space into two halves with opposite motor commands. The division by the two functions is orthogonal, and the lines on which opposite commands cancel both run through the goal (Figure 2.20). Mittelstaedt made no attempt to reproduce the systematic errors described above.

Matching these errors was one motivation for Müller and Wehner (1988). They first examined an algorithm similar to Jander's, that summed angles weighted not over time, but over (approximate) distance from the point of departure. They found that even for simple trajectories of one outbound leg and and a second leg of different length at some angle $\alpha$, the homing direction given by the mean-direction algorithm only fit experimental data reasonably well for $90° < \alpha < 120°$. They modified it by taking the angle from home as a reference, using a polynomial rather than linear function of angular deviation, and weighting it by distance from home, rather than distance travelled. The output of the resulting model agreed well with the systematic

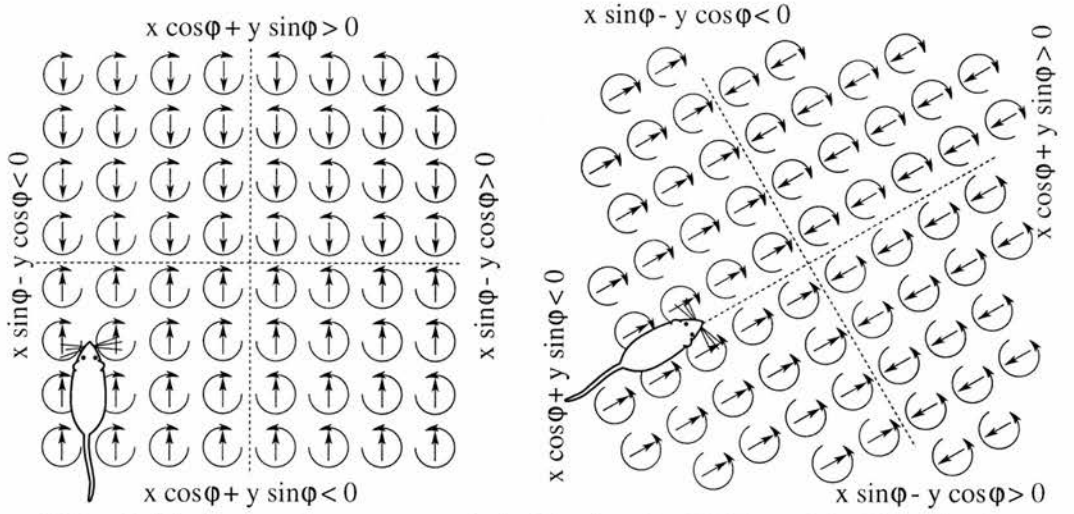



Figure 2.20. Field of run and turn commands in Mittelstaedt's (1985) model. The animal moves forward if x cosφ + y sin φ < 0, back if the sum is > 0. Analogously, it turns right or left depending on whether x sinφ - y cos φ is maller or largr than 0. This fields of commands is always aligned with the orientation of the animal. It turns and moves until it is on a line where x sinφ - y cos φ = 0 and there are no turn commands, then moves until x cosφ + y sin φ = 0 and there are no run commands. Mittelstaedt uses a coordinate system rotated 90° clockwise from that in figure 2.19, so φ = λ - 90°.

bias found experimentally. As Hartmann and Wehner (1995) later pointed out, the functions used by Müller and Wehner can be considered approximations to sine and cosine functions. Hartmann and Wehner used a sequence of straight line segments, derived from a neural implementation they proposed, to get similarly good agreement. Hartmann and Wehner's model also has a readout mechanism to return home, but it makes no provision for reading stored vectors.

Both these models use polar coordinate systems. In the absence of errors these are exactly equivalent, though the apparent convenience of computation may differ. Is it possible to distinguish between these two types of representation? Gallistel (1990 has argued that using a polar coordinate system, any error is not only added to the current estimate of position, it also enters into the computation of the next path increment. This argument only applies if there is noise in that feedback loop, a realistic assumption in any physical system, but especially biological ones. Nevertheless, it is not clear that this would result in behaviour different from that of a Cartesian system with more noise in the input. The coordinate systems do differ in the effect of approximations to trigonometric functions. Computation in a Cartesian coordinate system would have systematic biases that depend on the angle of the path to the reference direction. No such effect has ever been reported. In a polar coordinate system, the approximations lead to larger errors the closer a journey passes to the origin. Séguinot et al., (1993) studied the homing of hamsters on trajectories with either two or five outbound legs. The latter included conditions

where the hamsters went through a loop either close to or far from home, i.e. 1 m north, west, south and east either followed or preceded by a 2 m segment to the north. This made no difference to the hamsters. They homed with similar bias in both cases. The bias predicted by model of Müller and Wehner did depend on whether the journey passed close to the origin and failed to match the hamsters' behaviour only in the case of a loop close to home. In contrast, any errors due to approximation in a Cartesian system would be independent of location relative to the origin. The seeming contradictions can be reconciled by noting that systematic biases do not need to be accounted for by deviations from trigonometric functions. It is also possible that animals systematically underestimate the angles through which they have turned or that the bias is part of an error correcting strategy. The data of Séguinot et al. cannot distunguish between Cartesian and polar coordinate systems without approximations, but they suggest that if there are any approximations, their deviations from the exact functions are below random noise level.

A third approach is use of a map as in the models of Burgess and coworkers (see above) and McNaughton et al. (1996, discussed in chapter 3). They do not require multiplication by sine and cosine even for an exact solution. All that is needed is the distance and direction of each path increment, which must be added to the last position in the map.

Regardless of the details of the representation, path integration has two features that are relevant in the context of this thesis. First, the information is necessarily metric. Because it does not use location-specific cues, it cannot just identify some such cue from a distance and find a path taking the animal closer to that cue. The available information is direction of travel and speed or the length of path increments. The only way to use that information is to specify a location, *where* some place is.

Second, path integration is not possible by chains of associations. The reason lies in the combinatoric of two or three dimensional space. The only information available to a hypothetical associative path integrator is the sequence of steps leading to the current location. It would need to use that sequence to give each location a unique identifier. The problem is that each location can be reached by an infinite number of different sequences of steps. On the other hand, if the associative path integrator only looks back for a finite number of steps, then any given sequence can lead to any arbitrary location, given a suitable sequence beyond those the path integrator takes into account. Even if it could be made to work, this type of path integrator would take a long time to learn and so would be useless in unfamiliar

environments. Path integration must compute the current location of the animal. The isomorphism between representation and environment provided by associative learning cannot do that with the information used in path integration. Yet if learning is defined as the storage of information in memory, path integration clearly is learning. It is not possible to compute location unless the current path increment is added to the location stored in memory. Path integration or dead reckoning is an example of a navigational strategy requiring non-associative information storage.

Etienne et al. (1986) demonstrated that self-generated information (proprioceptive and vestibular) was sufficient for path integration in hamsters homing from a food hoarding site to their nest boxes. The hamsters lived alone in a nest box attached to the outside of the wall of a circular arena, with free access to the arena before the experiment. All experiments were conducted in the dark. The subjects were offered a pile of hazelnuts in the centre of the arena, which they collected for hoarding. In trials with an active outward journey the subject was led to the hoarding site, following a bait. In trials with a passive outward journey the animals stepped directly from the nest box into a transportation box and were carried to the centre of the arena.

The role of self-generated or idiothetic information, derived from vestibular and kinesthetic signals, and of possible intra- and extramaze cues was investigated by testing the animals' reactions to situations where these sources of information were in conflict. In the first experiment the arena with nest box was rotated during the subjects' passive outward journey. They homed in the direction of their start location as accurately as in the control trials without rotation, implying that they did not rely on intramaze cues. Passive transport to an adjacent arena did not affect the homing direction. The hamsters either used an external compass cue or integrated only passive rotations, but were unable to keep track of passive displacements. In a third experiment the orientation of the return journey was not influenced by alterations of the magnetic field. In the fourth experiment the arena and nest box were rotated by 90° before the passive or active outward journey, creating a conflict between self generated information and potential cues indicating the normal location of the nest box. The subjects' return to their actual start location indicates that they used only self-generated information. There was no evidence for use of an external compass cue.

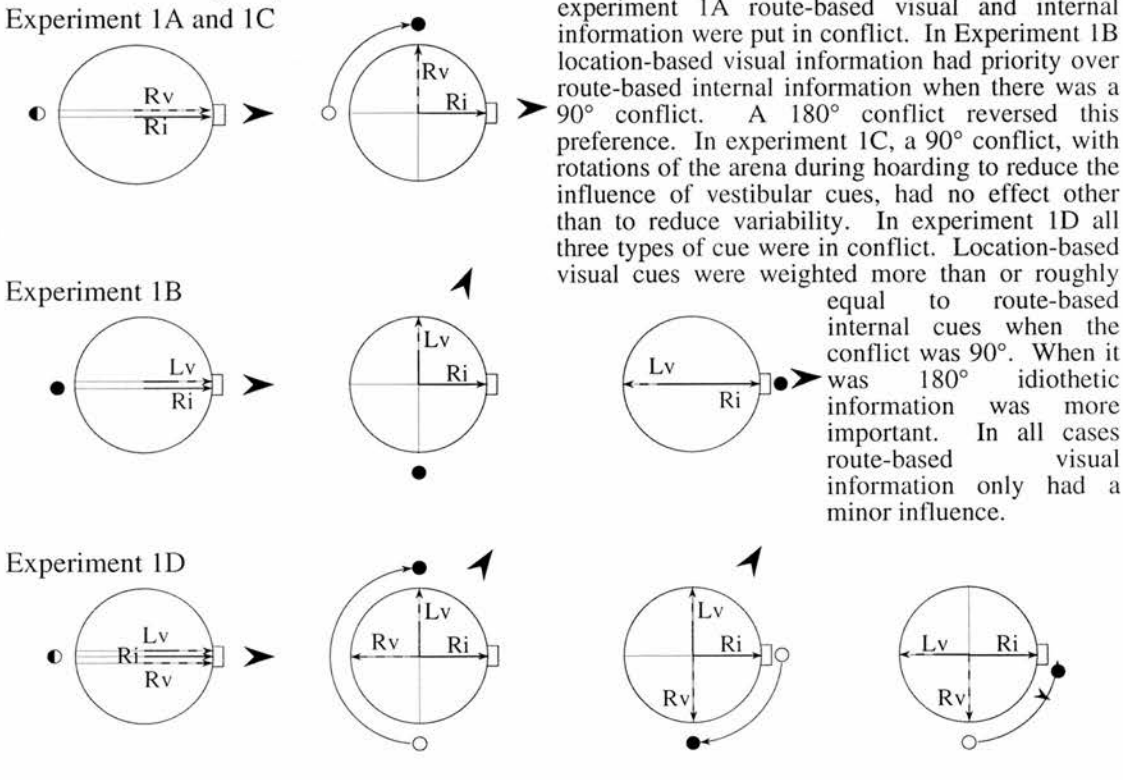
The authors make the further interesting point that "*experiments in progress show that the animal's capacity to compensate for passive rotations decreases in proportion to the amplitude of the angular displacements and ceases completely*

*when the animal has been rotated over more than two complete turns (i. e. 720°)*". Further, "*active rotations included in the outward journey are compensated for when they are up to three or five full turns, but lead to random orientation if they exceed this limit*". Collett et al. (1986) did not mention any attempt to eliminate vestibular cues. This may be their unidentified directional cue.

Etienne et al. (1990) investigated the effects of a conflict between a weak visual cue and self-generated information. They distinguish between three different types of spatial information: (1) location-based cues, which provide a stable and familiar frame of reference in the environment; (2) internally generated signals (proprioceptive and vestibular) used for path integration; (3) cues which are not in a consistent position in the long term, but may serve as a short term frame of reference. The latter two are classified as route-based cues.

The experiments were conducted in the same apparatus with similar procedures as in Etienne et al.'s (1986) study. The major difference was the presence of a very dim light source that served as a visual cue. It illuminated only a small area in the centre of the arena. The strategy in this study was to create conflicts between route-based and location-based information as well as between visual and idiothetic cues. If the hamsters had no experience with the light before the experiment, it could only

Figure 2.21. Summary of experiments 1A to 1D3 of Etienne et al. (1990). Small open circles show the location of the light cue during the outgoing trip, black circles the location from the moment hoarding began. The locations of the light and direction of rotation were normally counterbalanced, but are not shown here for simplicity. The arrowhead outside the arena shows the average homing direction. In experiment 1A route-based visual and internal information were put in conflict. In Experiment 1B location-based visual information had priority over route-based internal information when there was a 90° conflict. A 180° conflict reversed this preference. In experiment 1C, a 90° conflict, with rotations of the arena during hoarding to reduce the influence of vestibular cues, had no effect other than to reduce variability. In experiment 1D all three types of cue were in conflict. Location-based visual cues were weighted more than or roughly equal to route-based internal cues when the conflict was 90°. When it was 180° idiothetic information was more important. In all cases route-based visual information only had a minor influence.



function as a short term route-based visual cue (Rv). Rotation after hoarding had begun would put it in conflict with other cues. If the light had been experienced as stable, it could provide both route-based and location-based visual information (Lv). Visual information was exclusively location-based if the light was only switched on after the outward journey. It could be put in conflict with other information by putting the light cue in an unfamiliar direction. Idiothetic information must always be route-based (Ri) and was always present. Therefore it was only possible to put two combinations of two cue types in conflict (Rv/Ri or Lv/Li), or one type with the other two (Lv/[Rv, Li] or Rv/[Lv, Ri] or Ri/[Lv, Rv]) or all three (Lv/Rv/Ri). The results of the first series of experiments are summarised in Figure 2.21.

The animals gave roughly equal weight to visual location-based ($L_v$) and internal route-based ($R_i$) information if the conflict was 90°, while visual route-based ($R_v$) information has a minor influence. Increased conflict between the two preferred categories of information leads to increased reliance on self-generated cues.

In summary, the results suggest that, (1) a single light, presented in a standard position for some time before the experiment, comes to have a major effect as a location-based cue. (2) The light spot has only a minor effect as a source of visual route-based information. (3) Internal route-based information interacts with visual location-based information. The greater the conflict between the two types of information the more the hamsters rely on self-generated cues.

## 2.7. Summary

Models of navigational competence span the whole range from fairly simple snapshot models, requiring only simple associative processes, to O'Keefe and Nadel's definition of cognitive mapping, a rich representation supposedly constructed by different processes. Both these "standard" models make links between contents and conditions of learning that are not necessary. There are several models with at least some map-like properties that use at some point associative processes for the acquisition of information. Any conclusions regarding the relationship between navigation and associative learning must take that factor into account. It has also been shown that navigational systems may perform computations and construct representations with richer isomorphisms than those possible in associative learning.

# 3. Another (better?) way to make a map: Integrating spatial information from dead reckoning and landmarks

Navigation by use of snapshots, landmark-goal vectors or metric maps has so far been discussed separately from dead reckoning. Dead reckoning necessarily uses metric information, and its interaction even with non-metric landmark information can give a spatial representation some of the properties normally expected from a metric map. The various degrees of integration of spatial information from landmarks and dead reckoning are the topic of this chapter.

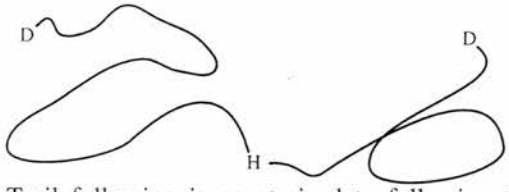
## 3.1. Navigational strategies

Possible navigational strategies are summarised in Figure 3.1. Use of trails and chemical gradients will be ignored here. The remaining strategies are ordered both by the kind of information they use and by an intuitive measure of complexity and the flexibility of behaviour they support.

Strictly speaking all dead reckoning must sometimes interact with location-specific information in order to reset to a known value and so remove accumulated randon errors. In its most basic form, a path integrator would only be able to reset at one location, probably home. To aid navigation to other locations, dead reckoning must be able to keep track of several location. The two methods mentioned in section 2.6 were use of multiple path integrators, each only resetting at one point, or else a path integrator capable of taking vectors retrieved from memory as input and which can be rest at any identifiable location. The latter method allows to improve the accuracy of the estimation of a location (identified through landmarks) by averaging the positions given through dead reckoning on separate visits to the same location. As this location becomes more accurately defined, it can serve as a reference point for resetting, and then improves the accuracy of navigation at neighbouring locations. This is not possible if multiple path integrators work independently and are each reset at only one point.

The purely landmark-based strategies (designated L in figure 3.1) could work in parallel with dead reckoning (DR). The assumption here is that only the final outputs of these systems would interact in determining behaviour. The integrated strategies (DL) involve a richer set of interactions, for example correcting dead reckoning by reference to landmarks, or using remembered metric information from dead

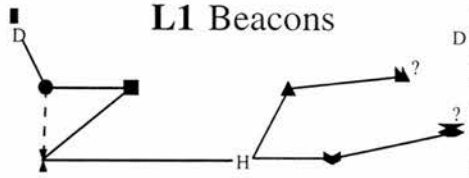
# Chemical trails




Trail following is constrained to following the path that was taken when a possible destination was encountered the first time, no matter how circuitous. To distinguish between destinations, different kinds of trail have to be laid down. There is no information at the outset how far away a destination is. What happens if there is a loop in that path? How does the animals decide which part of the trail to follow at the crossing?

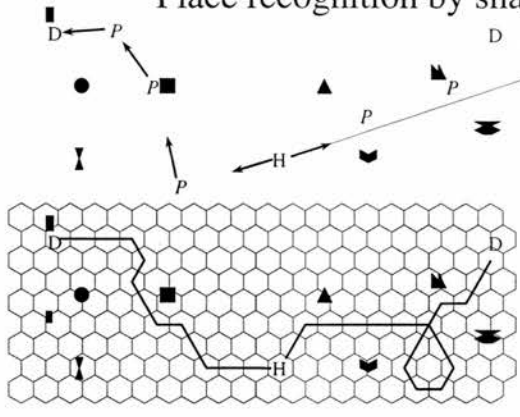
# Landmarks only (location-specific)

## L1 Beacons



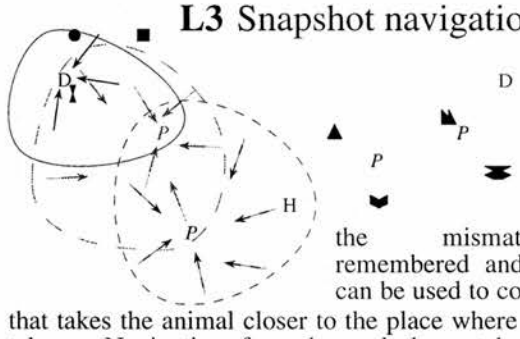

A beacon can be approached from any direction within the range where it is perceptible and recognisable. Beacons can be chained together into sequences. Where two beacons in a sequence are seen, the one further on can be chosen. But what happens if there is no beacon at a destination?

## L2 "Ballistic" S-R chains
## Place recognition by snapshot



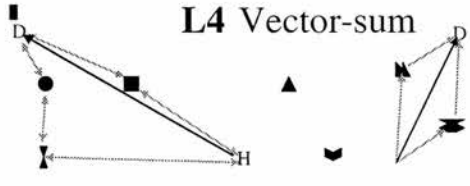

Places are recognised by snapshots and associated with a response of turning and going until hitting the next familiar place. If the density of such places is low, there is no error correction. If it is high (hexagons in lower diagram), the resulting representation could function as a map, but readout through S-R associations can only access a small fraction of that information.

## L3 Snapshot navigation




Snapshots can function as virtual beacons, each having a catchment area within which the mismatch between remembered and perceived view can be used to compute a direction that takes the animal closer to the place where the snapshot was taken. Navigation from beyond the catchment area of the destination requires stacks or sequences of snapshots in S-S chains. Distance to a destination is not known.

## L4 Vector-sum



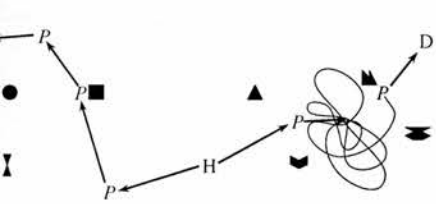

Addition of self-land-mark vectors, land-mark-destination and possibly intervening land-mark-landmark vectors gives a final self-destination vector. Shortcuts and detours (novel paths between familiar points) as well as instantaneous transfer (novel path from a novel starting point to a familiar destination) are possible. Vector lists may not be internally consistent.

## L5 Maps

Burgess and O'Keefe suggest a readout mechanism that can get a self-destination vector from a hippocampal place field map. It can only read one vector at a time and goal cells can only be generated while at the goal. Whether place fields are determined by snapshots (Sharp) by distance-tuned cells (Burgess et al.) or dead reckoning (McNaughton et al.) is not relevant to the readout, same as for the ballistic S-R mechanism.

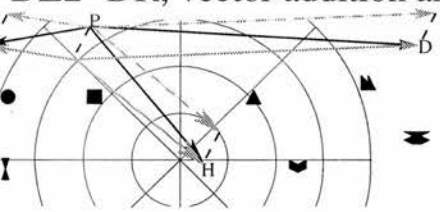
# Dead reckoning and landmarks

## DL1 Non-ballistic S-R chains




Place recognition by snapshot. S-R associations give both direction and length of the next path segment. Dead reckoning is needed for that, d the path integrator must be able to take a remembered ctor length as input. Vector addition is not necessary. An ror can be detected and search can be initiated. Both this and e ballistic S-R mechanism would benefit from snapshot vigation for error correction, as it would often make the arch shown here unnecessary.

## DL2 DR, vector addition and snapshots




Dead reckoning can be reset at specific locations recognised by snapshot. Storing home vectors makes it possible to average the ctors computed on successive visits to a place, removing ndom error from the estimated vector of that place. Addition vectors based on dead reckoning allows path planning. ror correction by snapshot navigation would speed up the ocess, but using snapshots only for place recognition, and itiating a random search, as above, is also possible.

## DL3 DR and vector-sum navigation

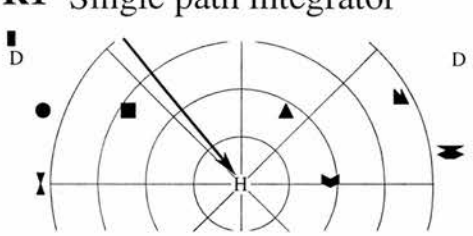
esetting of the path integrator is possible at any point, not here a snapshot has been taken. Path planning can be based both DR and landmarks. Vectors from both systems can go o a weighted vector sum.

## DL4 Dead reckoning and map

me properties as purely landmark-based map, except that vigation in unfamiliar areas is possible even without stantaneous transfer and even without seeing familiar ndmarks.

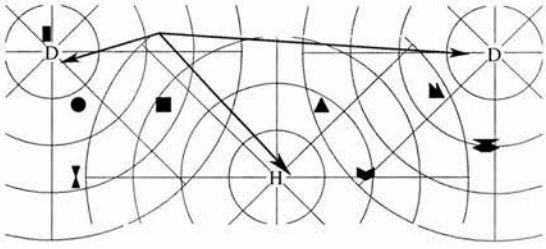
# Dead reckoning (location independent)

## DR1 Single path integrator



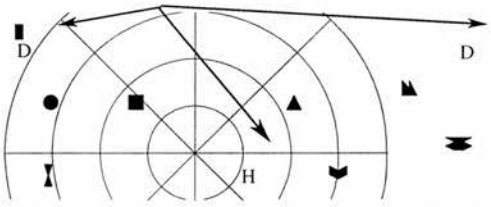

There is a single dead reckoning system or path integrator, shown (arbitrarily!) by a polar coordinate system, that can only be started and reset at one location, here home. No other locations can be tracked.

## DR2 Independent path integrators




Multiple independent path integrators could keep track of several locations. If each path integrator can only be rest at one location, errors accumulate independently.

## DR3 Single PI and vector addition




If the home vector of a location can be stored in long term memory, and later subtracted from the current home vector, it is possible to return to any location using the same path integrator. At any one moment the same error affects vectors to all locations. The location of the origin of a coordinate system is irrelevant.

gure 3.1. Classification of navigational strategies. Those labelled L4, L5, DL2, DL3 and DL4 are cognitive apping processes, by the criterion of including metric information and a capacity for vector addition, the erequisites for chosing between several goals on the basis of distance.

reckoning to plan a displacement if landmark information is non-metric. These interactions require at least that the output of a path integrator can be stored in long term memory, and that the readout mechanism can take vectors other than the current home vector as its input.

A route may be followed through stimulus-stimulus chains, without use of metric information, if at any recognisable place the next point of the route is perceptible, either in form of a beacon (strategy L1 in figure 3.1), or if the catchment area of the next snapshot extends to the current location (L3). If the next stimulus is out of range, the animal could use stimulus-response chains. The minimal requirement is that the animal can identify the correct direction, and then either risk moving until hitting the next familiar spot (L2), or moving for a known distance. The latter depends on dead reckoning to determine that distance (DL1). In its simplest form such an S-R scheme could rely exclusively on specific remembered vectors. Direction could be identified by storing the appropriate egocentric orientation of the snapshot. Each reference location would be the origin of a local coordinate system. As discussed for vectors between landmarks, storing vectors between all places of interest will lead to a combinatorial explosion. In the absence of a capacity for vector addition, the system would be limited to chaining vectors (in possibly novel sequences), but would have to follow each part of the resulting route rather than shortcutting straight to the destination. The estimate of travel distance would be the arithmetic sum of the lengths of the route components. It is also possible that a vector from A to B would be known, but not from B to A. This is a route based representation. These three strategies (L1, L2 and DL1) would not be considered cognitive maps.

Vector addition provides more flexibility. If vectors from visible landmarks to possible destinations are known, and the vectors from the current position to landmarks can be determined, an animal can determine its location relative to any remembered place (L4). As long as the relative locations and orientations of local references are known a global reference is not necessary. If metric information is derived from dead reckoning, it is not necessary to get it from landmarks. Assume a home vector is associated with each snapshot (DL2), and that the current home vector can be added to the inverse of the home vector of the desired destination (Cartwright and Collett, 1987). Within the limits of accuracy of dead reckoning any arbitrary path can be computed, including novel shortcuts and detours round obstacles, the distances between locations, the shortest paths between multiple locations, etc. Due

to the limited accuracy of path integration, resetting at locations other than home will be necessary. A snapshot cannot be used directly to correct any errors in the home vector associated with it because snapshots do not allow determination of distances by reference to visual landmarks. It would be possible to average homing vectors given by the path integrator on different visits to a place. This would improve the accuracy of the homing vectors, but only if the averaging occurs at the centre of a snapshot. At other points navigation by snapshot cannot determine the distance to the reference location which the home vector specifies. Use of metric landmark information (DL3) would only improve the accuracy of the system, but not change its properties otherwise. These three systems already have most of the properties of cognitive maps. Only two features are missing. One is that these vector based representations may not be internally consistent (see chapter 1, section 1.7, last paragraph). Second, as already mentioned, explicit representation of all possible spatial relations would is not very efficient, leading to a combinatorial explosion. Use of a global coordinate system would let the number of vectors grow only linearly with the number of places remembered, but has other problems (see section 2.5). Representing locations of objects and destinations only by reference to local coordinate systems would avoid these problems, while still slowing down the growth in the number of vectors to be represented. Use of vectors can introduce a binding problem. There may be several places sharing the same coordinate on one axis or direction. Each coordinate then would have several chunks of landmark information associated with it, and which is relevant would depend on the other coordinate.

The binding problem and combinatorial explosion can both be avoided by using a map rather than decomposing location into coordinates. A map would also be internally consistent. This is the approach of both Burgess and coworkers (L5 in figure 3.1) and of McNaughton et al. (1996; DL4). In Burgess' model an animal must visit a location before it can assign to it either a place cell or a goal cell. Goal cells can only connect to already established place cells. In McNaughton et al.'s model, the locations of all place fields in a reference frame are fixed as soon as as the location of one place field and the orientation of the frame are determined relative to landmarks. It may still be necessary to visit a place before landmark information can be associated with the place field. McNaughton et al are not explicit on that point. They also do not commit themselves on either metric landmark information or use of snapshots. Either is possible.

There is another capacity that could be added to all strategies using metric

landmark information, that is L4, L5, DL3 and, depending on assumptions, DL4. Using distance information from landmarks in principle allows the creation of an allocentric representation that could be used at any point where distance and direction of at least some of those landmarks can be determined. In the scheme of Figure 3.1, strategies L4, L5, DL3 and DL4 would be divided into two depending on whether this capacity for immediate transfer of knowledge to novel areas is present. It is taken to be a characteristic feature of cognitive maps by some authors (Whishaw, 1991; Alyan 1994). There is currently no evidence that this capacity exists.

Integrating landmark information with dead reckoning has some implications that are not immediately obvious. It pretty much forces use of multiple reference frames because a representation based on dead reckoning is necessarily preconfigured. It is not possible, as for example in Burgess' model, to arbitrarily distribute location-specific information all over the representing system. It must be assigned to specific elements as determined by dead reckoning (the model of McNaughton et al., 1996, provides a specific example and is discussed below). It is unlikely that the shape of an animal's territory will correspond to the shape of a global preconfigured representation it is born with. Parts of it may go unused while it may still not cover the whole territory. Or take the example of a species in which offspring is reared in the parents' territory, but disperses after some time. If the centre of the map were in the parental territory, after dispersal either a large part will go unused, or all landmark information will need to be replaced. The offspring may even go beyond range of the original map. If landmark information were added only after dispersal, individuals would have to make do without map while still in parental territory. It would also not solve the problem of being displaced from an established and mapped territory. A migrating species may need a map of two distant home ranges as well as of several way stations on the route between. Another problem could arise if two relatively close areas are normally reached via a detour, for example a central place forager that always returns home between visits, and the areas then become connected by a shorter route. Any cumulative errors in dead reckoning would introduce a discontinuity between dead reckoning and landmark information on the new route. A preconfigured global map would require realignment of all landmark information to deal with these problems, presumably a slow, costly and error-prone process. Using multiple reference frames, it is only necessary to pull out another frame. Their spatial relations relative to each other are presumably determined by shared landmarks. Multiple reference frames also naturally lend themselves to representation of the

environment at various different scales. Davis (1986) argues that this is necessary, as fine-grained representations have too much detail for large scale navigation and coarse grained representations not enough for accurate short range navigation. Evidence for the existence of multiple reference frames has been reported by Gothard et al. (1996)

The model of McNaughton et al. (1996) would be classified as DL4 in the suggested scheme. They proposed that navigational computations performed by the hippocampus are based primarily on dead reckoning and only secondarily on landmark information. The representation of space is essentially the same as the one discussed for Burgess' model: location-specific firing fields form patches of activity moving on a two-dimensional surface. As in Burgess' model, there is no coordinate system. Unlike that model the interactions between cells and the relative locations of their receptive fields are preconfigured. Even in the absence of any landmark information the place fields have predetermined spatial relationships relative to each other. McNaughton et al. also postulate the existence of multiple reference frames. It is assumed that on arrival in a new environment a rat will pull out a "blank" reference frame, consisting of an interconnected population of place cells not associated with landmark information. A reference direction is established and a place field in that reference frame is chosen as the initial location, according to unspecified criteria. From that moment the locations of all other place fields in this frame of reference are fixed, through their interconnections and their interaction with movement information.

What remains is the addition of landmark information. This is not described in any detail, but is assumed to be an associative process. In contrast to the Burgess model, it is not possible to arbitrarily assign landmarks to any place cell. Because the network is preconfigured, the learning rule must detect a given correlation between a landmark arrangement and place cell firing. This is the same computation as in conventional associative learning. Another difference to Burgess' model is that the amount of landmark information, only added secondarily, is unlikely to be homogeneous. Associative learning, being goal-driven, would ensure that only necessary information is added to the map. Poucet (1993) argued that such heterogeneity is a characteristic feature of spatial representations in relatively unfamiliar environments. He postulated that cognitive maps are created in a two-step process, first a topological representation linking a number of specific places, then metric information is filled in. The model of McNaughton et al. could be interpreted

as showing that the first step is based on dead reckoning and that the appearance of a topological map is a consequence of the inherent inaccuracies of dead reckoning not reset by landmark information. Alternatively, multiple reference frames could be initially only loosely connected and the representation appears to acquire metric information when the reference frames are bound together by shared landmarks or when large scale frames are established. Landmark information could be added in the form of snapshots, it could be vectors, or distances as in Burgess' model.

McNaughton et al. propose a neural mechanism for path integration. Direction and location do not interact directly with their derivatives, angular and linear velocity, but through intermediate cells, sensitive to both (Figure 3.2). The principle is easiest to illustrate for direction. A head direction input H and an angular velocity input H' converge on neurons that are sensitive to both, H'H. The signal for a particular velocity goes to H'H cells regardless of their direction, but specific to those with the correct velocity. The direction signal goes to all H'H cells responding to the correct direction, regardless of their velocity tuning. The resulting subset of H'H cells then can selectively activate the appropriate H cells, giving the new direction. McNaughton et al. suggest that velocity would be frequency coded, though position coding in a computational map (Knudsen et al., 1987; see appendix for illustration) would also be possible.

The advantages of using a map are the same as discussed previously for landmark maps: efficient storage of the spatial relations between large numbers of locations, no binding problem, and if goal cells are used for readout, they can quickly be linked to locations. For path integration there is the added bonus of avoiding multiplication of path increment and direction by sine or cosine functions.

The authors only specify the nature of the representation and the process by which it gets updated during dead reckoning. There is no description of a readout or navigation mechanism. The model would be compatible with the readout mechanism proposed by Burgess and O'Keefe (1995). It should be noted that in both models there is an anisotropy of available information. In the Burgess model this arises from the fact that information about *what* is at a place can only be accessed through goal cells. The map itself is homogeneous. In the model of McNaughton et al. there is an additional source of anisotropy in the distribution of landmark information. It would only be necessary to add that information to the map at intervals sufficiently short to allow resetting as often as required by the accuracy of navigation the animal needs. If resetting is possible through vector addition, the map would be functionally

isotropic

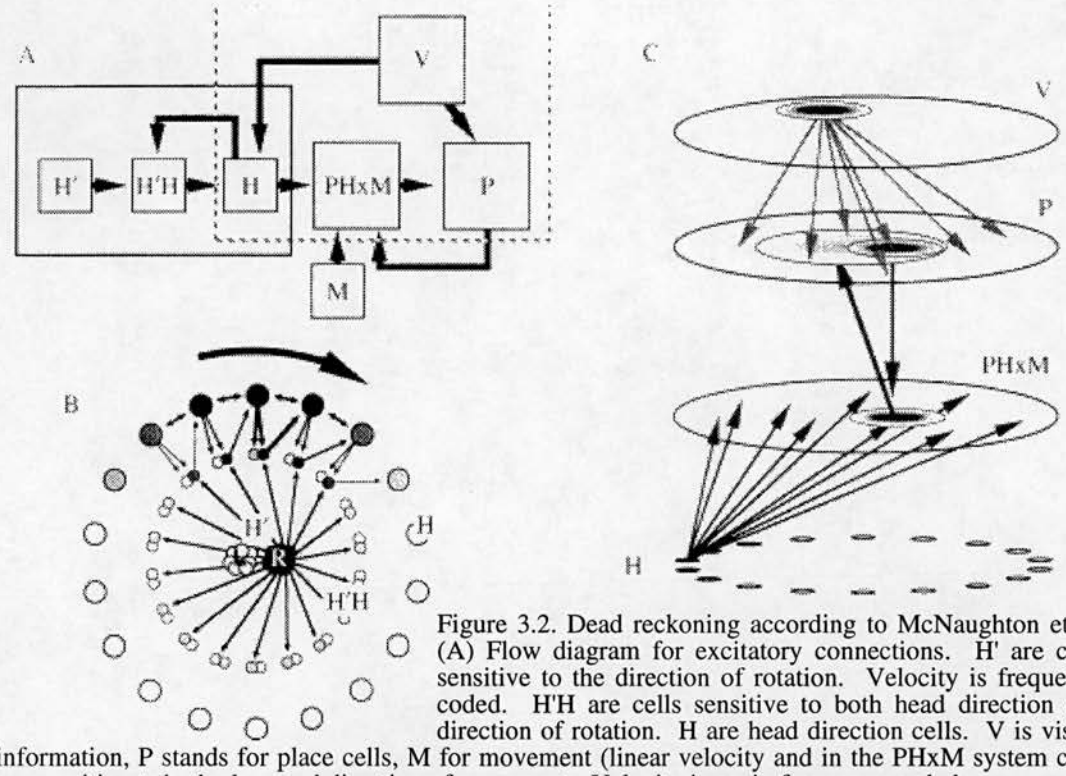



Figure 3.2. Dead reckoning according to McNaughton et al. (A) Flow diagram for excitatory connections. H' are cells sensitive to the direction of rotation. Velocity is frequency coded. H'H are cells sensitive to both head direction and direction of rotation. H are head direction cells. V is visual information, P stands for place cells, M for movement (linear velocity and in the PHxM system cells are sensitive to both place and direction of movement. Velocity is again frequency coded.
(B) The principle of updating is illustrated for the head direction system. In the H' system cells sensitive to turning right give input to all cells in the H'H system with the same tuning to rotation. Active head direction cells excites all cells in the H'H system with corresponding orientation tuning. Only those cells in the H'H system with convergent input from both H' and H systems exceed threshold. Their connections back to the H system goes to head direction cells with tuning appropriate for the rotation signal, in this case to the right. The faster the rotation, the higher the firing rates of H' and H'h cells.
(C) The PHxM system functions according to the same principle. Instead of two dimensions in the H'H system (head direction and rotation) it must deal with four dimensions (two dimensions of place, one of direction of travel, one of movement). Head direction information goes to all cells with approriate directional tuning anywhere in the PhxM system. Place cell input goes to all cells with the right place tuning, regardless of directional sensitivity. Only cells with convergent direction and place input exceed threshold. Movement signals are not shown, but must be diffuse over the whole PhxM system, regardless of place or direction tuning. That signal modulates the firing frequency of output from PHxM and so the speed with which the activity patch in the P system travels. In all cases topographic coding of location in space onto location in one of the systems is only for illustrative purposes. No such topographic coding has been found. For a computational argument, see appendix. Figure from Mcnaughton et al. (1996).

homogeneous.

## 3.2. Cognitive maps: Goal-independent representations and planning ahead

According to O'Keefe and Nadel (1978) two of the defining features of cognitive maps are their suitability for planning even novel routes, and their independence from goals, their creation being curiosity driven. Planning is meant to imply not only novel concatenations of elements, but the capacity to predict the cost of alternative routes and create efficient paths between multiple destinations. That requires metric information, as cost and efficiency are related to travel distance. With regard to the second feature, not only routes, but also the landmark-goal vectors of Collett et al.

(1986) are goal centered. In its simplest form a vector list would only contain information about the spatial relations between goals and visible landmarks. The spatial relations between landmarks or goals could be derived from addition of landmark-goal vectors sharing common points. Whether a spatial representation is goal-centered has implications for the kind of information that is added and the conditions under which learning occurs. This last point will be the topic of chapters 4 and 5.

*Is planning possible without metric information from landmarks?*

As discussed in chapter 2, bees' use of landmarks shows little sensitivity to distance, and what there is can be interpreted as matching by distance, rather than using this information for localisation. It is also widely, though not unanimously, accepted that bees have no cognitive map (Bennett, 1996; Collett, 1987; Dyer, 1991; Wehner and Menzel, 1990; Wehner et al., 1996). Yet when bees navigate dead reckoning and landmarks interact. Is that a case of S-R associations, with dead reckoning only providing the distance component of the response, or is their system more similar to a map built from integration of dead reckoning and snapshots, as described above? If the latter, what explains the limitations of bees' behaviour that have led to the assertion that they do not have cognitive maps?

In their waggle dances bees give both bearing and distance to food sources (von Frisch, 1967). Srinivasan et al. (1996) and Esch and Burns (1996) have reviewed evidence that the estimate of distance is derived from optic flow. In the experiments described by Srinivasan et al. bees were trained to find food at a set distance along a 12 cm wide and 20 cm high tunnel. The tunnel walls displayed vertical gratings that could be scrolled horizontally. It was found that bees kept constant the angular velocity of the image, independent of the spatial frequency or contrast of the gratings. Distance estimate depended critically on this angular velocity. When tested in a tunnel wider than during training, giving lower angular velocity, bees systematically underestimated the distance they had flown and carried on past the position of reward during training. Narrowing the tunnel had the opposite effect. When the grating was parallel to the length of the tunnel the bees were unable to estimate distance at all. Esch and Burns (1995) trained bees to fly to feeding stations at various heights above the ground, then observed their dances. First, they calibrated a distance curve by training the bees to feeders on the ground at a range of distances. Then a feeding station was suspended from a balloon at 70 m horizontal distance from the hive, and gradually raised it to heights of 30 m, 60 m and 90 m above ground. Bees flew

directly to the feeding station. As the straight line distance increased from 70 m over 76 m and 92 m to 114 m, the bees estimate of distance as communicated in their dances decreased from 70 m over 55m and 45 m to 25 m. This is despite the fact that the climb to the raised feeder station increased energy expenditure beyond that required for horizontal flights of the same length. Optic flow decreases with altitude, so distance estimates based on optic flow must decrease accordingly. Esch and Burn (1996) review other experiments along similar lines and argue that earlier studies claiming evidence for distance estimation by energy expenditure are consistent with the optic flow hypothesis if all experimental conditions are accounted for. Optic flow is location-independent information as it is not necessary to identify objects to measure optic flow or to know the distances between them. Optic flow is one of the inputs for dead reckoning, in bees probably the main input. Bees therefore use both distance information from dead reckoning and information from landmarks. Collett et al. (1993) also found that bees can learn sequences of motor responses and could retrieve them depending on the visual cues present. But do they simply combine this information in S-R associations, or are they capable of adding vectors, as suggested by Cartwright and Collett (1987)?

Menzel et al. (1996) describe a study (in prep.) of the interaction between vectors, motivational state and visual context. In a first experiment bees were trained to fly to a feeding station F1 in the morning and to a different feeding station F2 in the afternoon (Figure 3.3). F1 was in a fairly homogeneous environment, F2 in a more heterogeneous one. The motivational state depended on the point at which bees were captured before release from another site. Hive departing bees (HD) would have a goal vector pointing to F1 in the morning and to F2 in the afternoon. Feeder departing bees (F1D and F2D) would have the hive as destination. Hive arriving bees (HA) would have no destination stored in short term memory. Bees were captured and released at F2 in the morning and at F1 in the afternoon, the opposite of the training conditions. Hive arriving bees retrieved the bearing back to the hive at both F1 and F2, presumably cued by visual features. All hive departing bees retrieved the home vector at F2. From F1, where the surroundings were more homogenous, some bees flew back to the hive, some persisted flying on the bearing that would take them from home to their original destination F2. Feeder departing bees showed a distribution of departure bearings that at first sight appear counterintuitive. F1 departing bees kept kept to their original bearing even at the visually rich environment of F2. F2 departing bees showed a bimodal distribution at F1, some

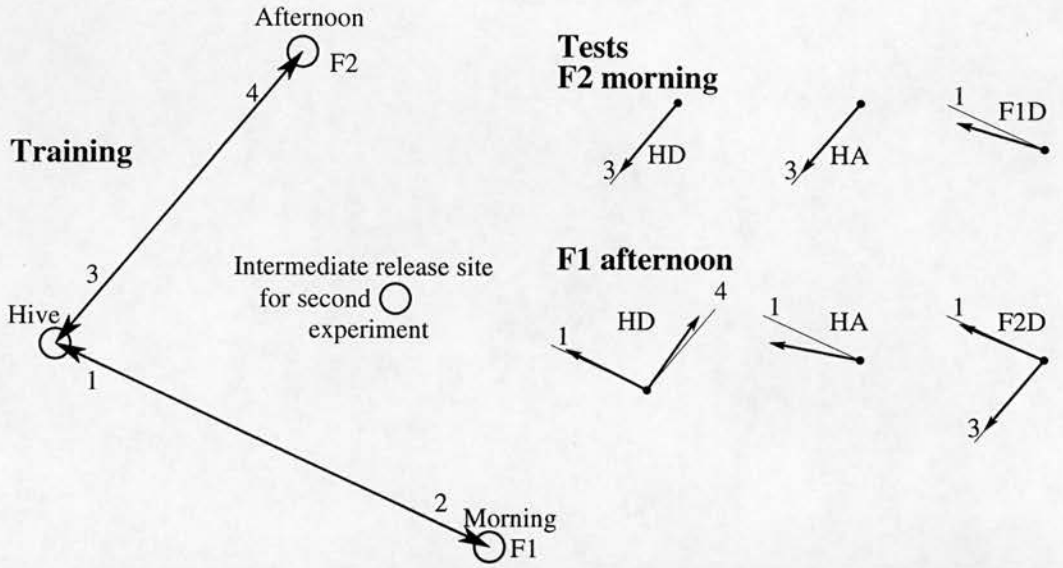



figure 3.3. Bees were trained to fly to feeding site F1, 790 m from the hive, in the morning and to feeding site F2, 630 m from the hive, in the afternoon. For testing bees were captured on departure from the hive (HD), departure from a feeding station (F1D), and arrival at the hive (HA). They were released at F2 in the morning and F1 in the afternoon, the opposite of training. The destination for feeder departing bees in the morning was vector 1. For hive departing bees it was vector 2. In the afternoon the respective vectors were 3 and 4. Hive arriving bees had no destination vector in memory. The diagram on the right shows the departure bearings for bees released at F2 and F1 for testing. Adapted from Menzel et al. (1996).

keeping their bearing, some adjusting it and flying directly towards the hive. This makes sense if it is assumed that the relative weights to be given to visual cues and to the currently stored vector are determined at the point of departure and not adjusted immediately after release somewhere else. Then some F2 departing bees, leaving a visually rich environment and giving more weight to visual cues, adjust when at F1. The F1 departing bees, lacking good visual cues at their point of departure, are set to rely on the remembered vector and do so even at F2. An important feature of these results is that hive departing bees do not add up vectors when finding themselves at the wrong feeding station. They either persist on the same heading or fly home. They never take the direct route between feeding stations. Judging by that experiment, bees seems to use S-R associations, retrieving vectors flexibly according to their surroundings.

However, another experiment in the same environment shows some capacity for vector addition. If hive departing bees, trained in the same way as before, are released at a site between F1 and F2, some persist flying on the F1 bearing in the morning and on the F2 bearing in the afternoon. Others added the two home vectors from F1 and F2 and successfully head back to the hive. Again, even though hive departing bees were motivated to fly to one of the feeding stations, they could not take the shortcut. The constraint seems to be that only home vectors can be added,

not a home vector and an outward vector. Menzel et al. suggest this is a restriction on the vectors that can be retrieved from memory. The classification in figure 3.1 does not have enough subdivisions to cover that. Using vector addition only on limited subsets of vectors puts it between DL1 and DL2. That behaviour was due to vector addition and not due to using the hive or some nearby landmark for a beacon, was shown by two controls. Bees released at a distant site did not just combine the two home vectors they had available, but persisted flying on the hive-F1 bearing. Bees trained only to F1 likewise had only one vector and experience with only one of the two sites. When released at the site between F1 and F2 they had no vectors to add up and no basis for generalising between F1 and F2. They persisted in flying on their original bearing.

Another line of evidence comes from studies of vector addition in bees (Collett and Baron, in press; Figure 3.4). Bees were trained to fly along two distinct vectors distinguished by two different background patterns serving as discriminatory stimuli. When given an intermediate background pattern, the bees averaged the two complete vectors, rather than direction and distance separately. If the length of the flight path had been determined visually, the bees should have averaged distance from the background pattern on the circular wall. The results not only show that whole vectors were averaged, they are also evidence that distance was determined by dead reckoning. Von Frisch (1967) found that bees trained to fly to a feeder via a detour nevertheless gave the direct bearing and distance in their dances.

Bees appear to have a spatial representation based on dead reckoning and snapshots (Cartwright and Collett 1987). Vectors can be retrieved by reference to visual information and combined. Sometimes this combination takes the form of

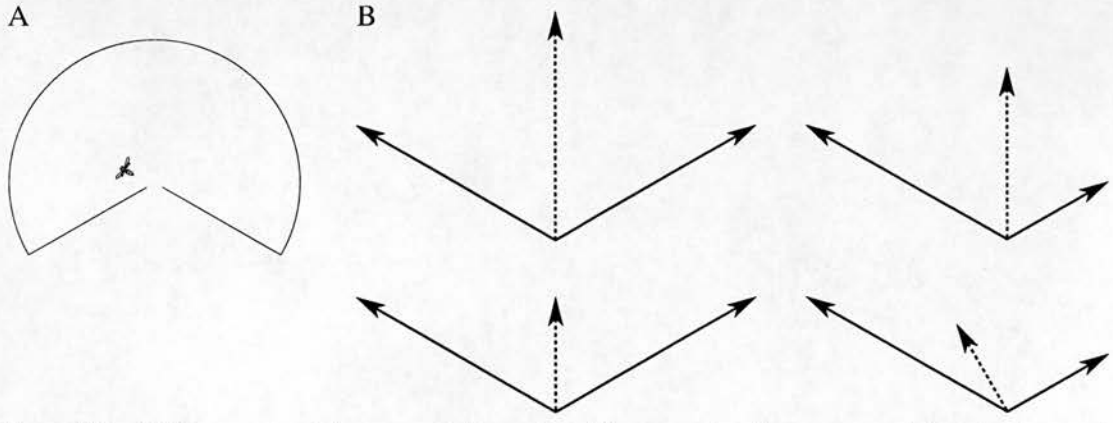



Figure 3.4. (A) Bees entered the arena at the centre. The curved wall was covered by a background pattern of slanted lines, which served as discriminatory stimulus. (B) Predicted results when averaging distance and direction separately (top row) or whole vectors (bottom row) after training to either vectors of equal lengths (left column) or different lengths (right column). The results of Collett and Baron (in press) were consistent with averaging of whole vectors.

concatenation or S-R chaining (Collett et al., 1993), sometimes vector addition or averaging are possible. The flexibility of the system appears limited only by constraints on the retrieval of vectors. Without those contraints this method of navigation should be capable of most planning postulated for a metric cognitive map.

*Shortcuts*

The most common test for the planning of routes is to offer subjects the opportunity of making novel shortcuts or forcing them onto detours. Many shortcut experiments are open to interpretations that do not require the postulation of a cognitive map. For example, Tolman et al. (1946) trained rats to traverse an L-shaped runway to a goal location directly under a bright light. When offered a choice between 12 routes, one of them replicating the familiar route, rats preferred a shortcut to the goal. While this distinguishes between repeating a motor programme and use of a landmark, it does not require use of a spatial representation. The rats only needed to recognise the light bulb and use it as a beacon. Likewise, Gould (1986) argued that bees were capable of making novel shortcuts that were only possible through use of a map, but Dyer (1991) found that bees could only make the shortcut if the destination was visible from the release point. The bees must have recognised landmarks at the destination and either used them directly as beacons, or they were within the catchment area of the relevant snapshot. Bennett (1996) concludes from this refutation of Gould's claim, a similar interpretation of the results of Chapuis et al. (1983, 1987) and the general argument that shortcuts can be accounted for by previous experience, recognising landmarks at the destination or dead reckoning, that no truly novel shortcut has ever been conclusively demonstrated. He argues that therefore there is no conclusive evidence for the existence of a cognitive map as described by Tolman and O'Keefe and Nadel. His argument that dead reckoning is an alternative method for making shortcuts relies on the assumption that it is an alternative strategy, simpler than mapping and used only in parallel and in competition with mapping. It does not allow for the possibility that dead reckoning may be an integral part of a cognitive map, as suggested, for example, by O'Keefe (1976), McNaughton et al. (1996) and discussed here in section 3.1.

In fact, one feature of the results of Chapuis and Varlet (1987) suggests an interesting interaction between use of landmarks and dead reckoning. Dogs were led 24 m to a point A where they were shown a piece of meat. They were led back to the starting point and then along a 40 m path, at a 30° angle to the first one, to a point B with more meat. The locations of A and B were varied so that the dogs were never

led to any point more than twice, and points were selected so that there were no conspicuous landmarks at or near them. When released at the starting point, the dogs normally ran to A and from there took a shortcut to B. If the path deviated no more than 5° from a straight line between A and B it was classified as a direct shortcut. If it deviated by more than 5° towards the starting point it was an inside shortcut, if it deviated in the other direction, an outside shortcut. Both in a homogeneous and a heterogeneous environment there were more inside than outside shortcuts. Interestingly, there were fewer direct and more inside shortcuts in the heterogeneous than in the homogeneous environment, although landmark-based navigation should be easier in the heterogeneous environment and shortcuts more accurate. Chapuis and Varlet suggest that this is an error correcting strategy. The inside shortcut takes the dog onto the path from start to B, which it has traversed a short time before. In the homogeneous environment there was less information available to recognise the path, so this strategy would not have been useful. The dogs took more direct shortcuts, presumably relying more on dead reckoning. This would be an example of an error correcting strategy, sensitive to how much information is available for correction. It is presumably dependent on information regarding the likely size of the random error due to dead reckoning, and the paradigm might be used to study the representation of uncertainty in navigation. The result also raises the possibility that the systematic errors found in dead reckoning (see section 2.4) are part of such an error correcting strategy, rather than errors in computation.

*Other path planning*

Bennett's emphasis on shortcuts as a defining feature of cognitive maps appears misplaced. Shortcuts are not the only possible example of planning trajectories, as shown by the approach of M. F. Brown and coworkers. Brown (1992) compared the performance of rats in a 12-arm radial maze with a model that assumed that after leaving an arm a rat would chose the next arm to investigate at random (within their average arm separation bias). Visual inspection (a microchoice) will result in rejection or walking down the arm (a macrochoice). Choices can be further subdivided in hits (correct macrochoice), false alarms (incorrect macrochoice or false positive), misses (incorrect microchoice or false negative) and correct rejections. Using empirically established response biases, mean hit rates and false alarm rates, the model closely matched the rats' behaviour without assuming that microchoices were guided by prior knowledge of unvisited arms. Reference to a map was not necessary to explain performance.

However, two later studies (Brown and Huggins, 1993; Brown and Lesniak-Karpak, 1993) showed that maze arm length, angle of inclination and brightness can influence choice criteria. If a lax choice criterion is applied, for example, to short arms because the cost of walking down to the end is low, then hit rates should rise and correct rejection rates should fall. In contrast, if short arms are harder to discriminate, then both hit rates and correct rejection rates should fall. By analogy, rats may have a map, but the cost of microchoices may be so low that the rats prefer to sample the visual scene and compare it to memory rather than referring to the map and restricting their microchoices to those arms that are likely to be unvisited. If the cost of sampling is sufficiently high, guidance of microchoices by a map will result in greater efficiency. There will be fewer microchoices leading up to a correct macrochoice.

Brown et al (1993) investigated this possibility by manipulating access to visual cues. They found that guidance of microchoices depended strongly on the cost of access to extramaze cues. Some data suggested that this was an effect of choice criterion. Guidance did not differ between reference and working memory. Under restricted view conditions intramaze cues had some influence, but did not exclusively control behaviour. It appears that there is a representation that allows planning of spatial behaviour, but it is not used for that purpose if relevant information is easily available at the choice point.

A different approach was pursued by S. W. Brown and Mellgren (1994), who attempted to distinguish representations of paths and destinations, in order to test a particular type of cognitive mapping theory, the world graph model (Lieblich and Arbib, 1982). It predicts that more information is available about places of interest than about the paths leading there. They let rats forage on a two-storey four arm radial maze. The rats started from a central platform on the lower level. Each of the four arms had a ladder leading either to a central platform or to four peripheral or dispersed platforms. The rats could take four different routes to the same place, or to four different places. The information available at the choice point was the same in either case. If food was replaced after each visit there was no incentive to alternate choices. The Dispersed group nevertheless showed spontaneous alternation while the Central group was at chance. Rewarding alternation in the Central condition raised alternation, but not to the level of the Dispersed group without reward contingency. Partitioning the central platform raised spontaneous alternation to the same level as in the Dispersed group, above the level of a group foraging at an unpartitioned central

platform. In this case the partitioned and unpartitioned Central groups had not only the same information at the choice point, but their routes were also identical. The results show that information about destinations is available when choices are made. In Rescorla's terms, they exclude a pure S-R model and require at least an association of the stimulus with a response-outcome complex.

*Instantaneous transfer*

Another aspect of the planning of novel trajectories is the question of transfer of knowledge to unfamiliar areas. In the shortcut studies the question was whether animals could find a novel route between familiar points. Here the question is whether animals can reach a destination from an unfamiliar starting point. Morris (1981) trained rats in the watermaze to find the escape platform from the same start point in trial after trial. When some animals were started from other positions their latencies to reach the platform were no longer than those of a control group. Morris argued that this instantaneous transfer to a novel starting point favours a cognitive mapping account, but Sutherland et al. (1987) pointed out that the starting points were not entirely novel in that they had been traversed by the rats early in training, when their search paths still covered much of the pool. Consequently, in one of their experiments they used clear or opaque partitions to restrict rats' access to either visual cues or parts of the pool or both. They found that a clear partition, dividing the pool and making continuous trajectories between the two halves impossible, was sufficient to prevent transfer to a new starting position, even if rats had been given separate swimming experience in that area. Sutherland et al. concluded that to exhibit transfer of efficient navigation to a novel start position rats must "(1) be familiar with the distal cues viewed from the region of the novel starting location, and (2) swim through the vicinity of the novel starting location as part of a swim path associated with the invisible goal". However, close examination of their figure 3 suggests this is not the case. The group of interest is one that had a clear partition, and swimming experience in both halves of the pool. Only swimming in one half could lead to the platform during training. This group therefore satisfied criterion 1, but not criterion 2. If Sutherland et al. are correct, then rats in this group should be inaccurate while in the half of the pool from which they could not swim to the platform during training, but should be accurate once they reach the half where swim paths were associated with the goal. The swim path selected as representative shows the opposite pattern. The rats head for the correct quadrant from the novel starting position, but are inaccurate when in that quadrant. The experimental design has a problem that may

account for this behaviour: removal of even a clear partition alters the shape of the environment, which Cheng (1984) claims to be an important feature of spatial representations. For this reason I do not accept Sutherland et al.'s interpretation, or the argument by M. A. Brown and Sharp (1995) that this result supports an S-R account of navigation.

Keith and McVety (1988) investigated instantaneous transfer using a latent learning paradigm. Rats were trained in a watermaze for three days, each day with a different platform position. Three groups were placed on the platform before each trial to view the environment from the goal. A fourth group did not have this opportunity. In a second phase rats searched for a platform in a pool in a completely unfamiliar room. Those who were placed on the platform before this test showed substantially shorter latencies compared to a group without placement in phase 2 (less than 10 s versus 33 s), as well as a higher probability of entering the target quadrant first. This did not depend on their receiving platform placements in phase 1. A group placed on a platform in a different location from the one during the actual test trial showed intermediate latencies, presumably having learned something nonspecific such as that a platform is present or its distance from the wall. Keith and McVety therefore argued that "the knowledge system that subserves place learning is independent of the behavioural actions the animal must initiate to find the platform". In other words, rats can locate the platform without learning a path first, contrary to Sutherland et al.'s argument.

This claim was disputed by Chew et al. (1989) and later Whishaw (1991), who argued that instantaneous transfer meant not merely significant improvement in a novel environment after a single placement trial, but "accurate navigation". This they defined as reaching the platform within 4 - 5 s while travelling in a straight line, i.e. an asymptotic performance level. The definition confuses the properties of a representation with the conditions of acquisition of information. First, it assumes that all relevant information can be obtained from a nearly static view, despite the fact that a swim trial would give additional distance information from motion parallax and looming. Second, even given that information, there is likely to be some sampling error under most conditions. A cognitive map could only be used to create accurate trajectories once it contains accurate information.

Whishaw (1991) also used a latent learning paradigm, in an extensive series of experiments varying the number of platform placements and the interval between placement and swimming. Single placements improved performance and were found

to be as effective as 5 placements prior to swimming, but after 15 placements there was no benefit compared to a no placement group. To keep the following discussion simple, only results from groups that benefited most from placement will be compared to the no placement control group, without distinguishing between placement intervals. Whishaw first trained rats for 15 days in the same pool, swimming twice per day from the same starting point, to a different platform location each day. Placement groups had lower latencies and fewer deviations from a straight line, but comparison of their first trials with the no placement group's second trials showed that placement was less effective than a swimming trial. Still, even that single swimming trial did not lead to accurate performance by Whishaw's criteria. Latencies were above 10 seconds and the probability of errors mostly above 0.5. Swimming and placement were additive, as shown by comparing the second trials of all groups. Placement groups performed better in that comparison. A placement trial also improved performance in a new environment, but the improvement was less and latencies in placement groups higher than those found by Keith and McVety.

Whishaw argued again that the lack of instantaneous transfer by his criteria and the additive effects of placement and swimming constitute evidence against a cognitive mapping account. For the reasons outlined above, this is wrong. Further, swimming even in a familiar environment to a new location did not lead to accurate performance, demonstrating that there were sampling errors after a single exposure. Therefore a placement trial, giving less opportunity to use motion parallax and looming, could not even in principle be expected to lead to accurate performance by Whishaw's criteria. Finally, a cognitive map is not the only alternative to an S-R model. A sufficiently detailed snapshot could, in principle, be used to generate even an "accurate" trajectory after a single exposure. The latent learning paradigm used by Keith and McVety and by Whishaw cannot distinguish between associative and cognitive mapping accounts, only between use of information acquired while moving or stationary at the destination. Distinction of information specific to a particular route from use of motion parallax to create a spatial representation would require further modification of experimental design. One possibility is adding a second trial in the novel environment to Keith and McVety's experimental design. Only rats that had a trajectory not leaving the target quadrant would be selected for the second trial. Half would be started from the same point as in the first trial, half from the opposite location. If an S-R mechanism were exclusively responsible for navigation, the trajectory from the novel starting point would be as long as that in the first trial after

placement. If path-specific information contributes, then the path from the novel starting point should be longer than that from the familiar one in the second trial. If the use of motion parallax makes the difference between placement and swim trials, there should be no difference between novel and familiar paths in the second trial. All transport of rats would have to control for dead reckoning, which none of these experiments has done.

This is relevant because Alyan (1994) found that mice could home after passive displacement in an environment only familiar from a stationary view (similar to a placement trial in the studies discussed above), if optic flow was available. If they were transported passively while eliminating optic flow and other possible information for path integration, homing direction was random. A snapshot was not sufficient to support homing under these conditions. In a further experiment, mice had 24 hours to explore a rectangular arena with full view of visual cues in the room. Then they were transported, while eliminating dead reckoning, to a nearby arena. Each mouse spent another 24 hours in a nest box with an exit at the periphery of that arena, enclosed by a transparent cylinder that only allowed a static view of arena and landmarks. If mice were then displaced to the centre of the arena, without opportunity for path integration, their homing directions were random. Therefore comparison of information acquired in one region of the room with a static view of another region was not sufficient to include it in an overall map. This kind of capacity has, to my knowledge, not been conclusively demonstrated, while Alyan's study offers evidence against it at least in mice.

There is one other aspect of path planning that can, in principle, distinguish between use of snapshots and S-R models on the one hand and metric representations of space on the other. That is planning of optimal trajectories between multiple goals. Menzel (1973) found that chimpanzees who were carried by a human who was hiding food at 18 locations in a familiar area were able to recover the food following a completely different and more efficient path. These data were not analysed as to how far ahead the animals must have looked in their choices. They may have simply picked the next closest location.

*Implications of memory load for maps and lists*

One aspect of whether representations are goal-centered or not concerns the kind of information that is acquired. It appears reasonable that a goal-centered representation should only include as much information as is necessary to find the goal. In the case of vector lists, one might expect that only landmark-goal vectors are

stored, and perhaps just enough vectors between landmarks to identify an array. If spatial information is stored in a map, memory load is only proportional to the numver of locations stored. The presence of a very rich representation might be taken to favour maps over vector lists. The patterns of exploration in the experiments of Poucet et al. (1986) and Thinus-Blanc et al. (1987) led to the speculation that animals may represent spatial relations that do not directly correspond to the relations between perceptible objects in the environment. In this specific case hamsters may have had knowledge of the shape of an empty area inside an array of landmarks and were able to reconstruct this shape even when a landmark was missing or had been displaced away from the empty area.

A similar effect was found by Dallal and Meck (1990), when they trained rats with a consistent pattern of eight baited and four unbaited arms on a radial maze. After initial training there was an interval of approximately three weeks, then the rats were housed, trained and tested in a different environment. They were split into Reversal and Nonreversal groups. The former was tested with a different pattern of baited and unbaited arms, leading to a reversal of status of 50-67% of arms. The Nonreversal group was tested with the original pattern of baited and unbaited arms. Rats in the Nonreversal group showed no significant decrement as a result of transfer to a new environment, while the Reversal group's performance was worse than during the final days of training in the original environment. The difference between groups was significant. If the rats had coded the pattern of baited and unbaited arms only with reference to visible features, information regarding the locations of food items relative to each other could only be retrieved in the presence of those features. The fact that transfer of information to a new environment occurred favours the alternative, a representation that includes information of the relative locations of all points of interest. A related effect was reported by McLaren (1991), who found that after making four forced choices in a radial maze rats performed better in the following four free choices if the forced choices had been in a symmetrical pattern. This could only make a difference if spatial relations between chosen arms were represented, rather than only between arms and landmarks. If all such spatial relations were stored as a list of vectors, there would be the danger of combinatorial explosion discussed previously. A map storing metric relations only implicitly would not suffer from this problem. Therefore evidence that information is available about spatial relations not only between unmarked locations and visible landmarks, but also between different unmarked locations, can be taken to favour map-like

representations over vector lists. However, this is only an efficiency argument, not conclusive evidence. The conditions of learning will be discussed in chapters 4 and 5.

## 3.3. Summary

Information from dead reckoning and from landmarks has complementary properties. Dead reckoning uses information that is not location-specific and can therefore be used immediately even in unfamiliar environments. The information is metric, permitting determination of *where* places are and, given the capacity to perform vector addition, also how far apart and what the cost of travelling between them. Dead reckoning's disadvantage is the accumulation of random errors. It needs to be reset by reference to location-specific information, available from landmarks. Even if that landmark information is not itself metric, it can still give a reference for resetting by providing an anchor point where the dead reckoning information on successive visits can be averaged, removing most of the random variation.

Several possible ways of integrating landmark information and dead reckoning allow planning of novel routes, one of the features said to define a cognitive map. Other possible criteria are efficient coding, with the number of stored variables only growing linearly with the number of stored places, and perhaps no decomposition of location into the components of a coordinate. Each of these criteria would narrow down the number of systems that would be called a map. There is evidence that bees reset dead reckoning by reference to landmarks and add vectors based on dead reckoning, though with limited flexibility. As reviewed in the last chapter, rodents and birds use metric information from landmarks, and are able to complete planned trajectories without visual feedback, presumably using path integration. There is also evidence for choice between multiple destinations based on a spatial representation, and that this includes information about destinations, not only routes. I suggest that much of the dispute over what constitutes evidence for the existence of a cognitive map (for example, Bennett, 1996) stems from the use of different and not explicitly defined criteria. The proposed classification of possible cognitive maps might form the basis of definitions sufficiently precise to convince even Bennett that the term 'cognitive map' is meaningful.

# 4. Landmark Stability

In order to achieve good cue control for a blocking experiment, initially the procedures of Collett et al (1986) were followed by moving landmarks from trial to trial to establish them as the only reliable predictors of reward location in an open field maze. After two unsuccessful pilot studies it was found that animals did show focused search, controlled by the landmarks, if the landmarks were stable throughout training. This conforms to O'Keefe and Nadel's (1978) prediction that "variability makes it difficult, if not impossible, to build a useful map". The studies, by Kraemer et al. (1983) and Spetch and Honig (1988), also indicated a detrimental effect of instability on spatial learning. In contrast, it is usually found in associative learning that animals concentrate on the best predictor of a stimulus, to the detriment of learning about other signals. The classic exemplars of this latter principle are the experiments by Rescorla (1968) and Wagner et al. (1968). Rescorla varied how well a target stimulus predicted that reinforcement would occur. Wagner et al. varied how well other stimuli predicted reinforcement while keeping constant the conditional relationship between the target stimulus and reinforcement. In that respect, the following experiments on landmark stability, conducted with Dr. R. G. M. Morris, are analogous to those of Wagner et al., excepting that we explored the effects of systematic variation of spatial, not conditional, relationships. As in Wagner et al.'s experiment, the relationship between the target cue and reward, in our case the distance to landmark(s), and the direction relative to landmark(s) and polarising cues, were the same in a stable or Fixed and in an unstable or Varied condition. The difference between conditions lay in how informative the non-target cues were with respect to the location of reward. The less informative cues other than the landmarks were, the less they should be able to compete with the landmarks. A further difference to Wagner et al's experiment lies in the fact that our non-target cues must be the larger frame of reference, rather than another landmark. Only if there is that larger frame of reference is there any basis for classifying the target landmark(s) as stable or unstable. In other words, we explored a spatial analog of relative validity and not, strictly speaking, relative validity itself. The experiments also differed crucially from those of Kraemer et al and Spetch and Honig, where there was no clear separation of stable and unstable landmarks, and the tasks only required discrimination of discretely marked locations, rather than navigation to unmarked ones. If a stable reference frame were clearly separated from the unstable one, without spatial overlap, that limited stability might be sufficient to support spatial

learning. If there was still no learning, this result would provide a stronger argument that stability is an important feature in spatial learning. Furthermore, it cannot be taken for granted that the processes engaged by a spatial discrimination are in all respects identical to those used in navigation. The effects of landmark stability or lack of it had not been established and it was decided to investigate this issue before returning to the study of blocking in the spatial domain. The experiments described below were designed to test the effect of instability on learning rather than asymptotic performance, to clearly separate stable and unstable cues, and they required navigation rather than discrete choices.

## 4.1. Experiment 1: Landmark stability and dissociation of spatial learning and discrimination

### Methods

*Subjects* The subjects (N=16) were experimentally naive male Lister hooded rats which, through controlled feeding, were maintained at 85% of their free feeding weight. One animal in each group was dropped from the experiment after day 4 because they failed to eat the reward, leaving group sizes of 7.

*Apparatus* The experiments were conducted in a 3.3m by 3.3m square arena, with 40cm high white walls and filled to a height of 5cm with wood shavings. This arena was set within a larger square room with black walls and surrounded by movable ceiling-to-floor curtains. These curtains were black on three sides and white on the remaining side. The orientation of the white curtain - the polarising cue - was varied between days in a random sequence, with the constraint that all orientations occurred equally often and none twice in a row. Although not geocentrically stable, it will be referred to as "North". During training trials the arena contained two feeders and two landmarks placed at specific locations

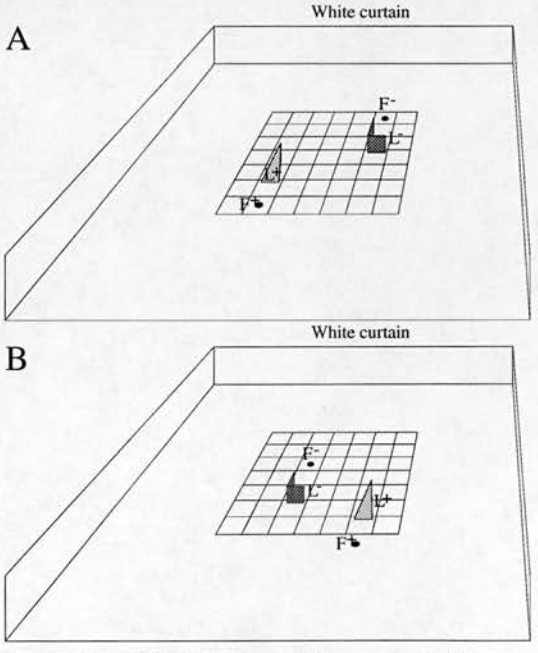



Figure 4.1. (A) Diagram of the open field maze. It is a square enclo-sure measuring 3.3 m each side. Feeders were placed 40 cm N or S of L+ and L- respectively. (B) In the Varied group these two landmark -feeder arrays moved independently and at random so that the landmarks stayed within a 7 x 7 grid of discrete positions.

(Fig 4.1.).

The feeders were made of chrome tube, 5cm long and 19mm diameter, mounted on a plywood base Both contained an equivalent amount of the cereal "Kellogg's Coco Pops" as reward. In one feeder, designated F+, this reward rested on a 4.1cm long wooden dowel and was thus accessible to the rats. In the other feeder, F-, the dowel was only 8mm long, and the food consequently inaccessible. When in place, all but the top surface of the feeders was beneath the wood shavings.

The two landmarks had distinctive shapes, textures and odours. L1 was a tetrahedron with unequal surfaces, covered with sandpaper on which 1ml of strawberry flavouring was added at the beginning of each training session. L2 consisted of two low carpet-covered plywood walls arranged in an L-shape with 1ml of added coffee flavouring. Either of these landmarks could be L+, defined as the landmark nearest the feeder with the accessible reward. In each group of 7 rats, 4 were trained with L1 as L+ and L2 as L- and 3 were trained with L2 as L+ and L1 as L-. Two near-identical copies of each landmark were used alternately throughout training in order to equate exposure prior to an end-of-training "identical landmarks test".

Each feeder was located at a distance of 40 cm from its corresponding landmark. F+ was always to the south (ie. opposite the white curtain) of L+ and F- to the north of L-. The spatial relations within each landmark-feeder array and its orientation relative to the polarising cue were always constant.

The movements of the animals in the arena were monitored by an overhead video camera, connected to an HVS image analyser and an Acorn A5000 microcomputer housed in an adjacent room. Custom software recorded the time taken to find the food and displayed, in real-time, the paths taken by the rats as a series of x,y coordinates (Spooner et al., 1994). Analysis of time spent searching at specific locations was later conducted off-line.

*Procedure* Pretraining: Before the start of training the rats had 10 days of handling and, in a separate cage in the animal house, were trained to eat from the feeder. This was followed by two days of 30 min habituation in the empty maze (no landmarks or feeders), first in pairs, then individually.

Training: The animals were divided into 2 groups. In Group Fixed, both landmark-feeder arrays (L+F+ and L-F-) stayed in a consistent position in the arena throughout training. In Group Varied, the two landmark-feeder arrays were moved to a new position after each trial with their orientation relative to the polarising cue the

same in all trials. The sequence of positions of the L+F+ and L-F- arrays was random, within the central 7 x 7 grid, subject only to the constraint that a landmark was not allowed to occupy a position adjacent to that of a feeder (in a completely random positioning sequence, this would have been possible as the two arrays moved independently). The adequacy of this design and those of the following experiments relies on subjects extracting a location-independent reference direction from the polarising cues (Taube et al. 1990a; Taube et al. 1990b).

The training procedure lasted for 22 days with 5 trials per day. The rats started a trial at the centre of and facing one of the walls in a quasi-random sequence, with the constraints that the start positions were used equally often and each at least once a day. A trial ended when the rat found the food, or after 120 sec, whichever was the shorter. A rat which failed to find the food within 120 sec was picked up and placed in front of the feeder up to 3 times or until it ate. The feeder was then refilled and the bedding thoroughly shuffled before the next rat was put in the maze. One nonrewarded trial, of 60 sec duration in which neither food nor landmarks were present, was intermixed with normal training trials each day. Thus, of the 5 trials per day, 4 were rewarded and 1 nonrewarded.

The animals were run in groups of 7, so the intertrial interval (ITI) for each particular animal depended on the latency of the others, declining from about 30 min at the beginning of training to about 20 min at the end. The subjects were transported to the start locations in an opaque, slowly rotating box to prevent them from using vestibular cues or any other directional cues outside the arena. They were removed from the arena at the end of a trial in the same box.

*Transfer Tests* Once a stable level of performance had been attained, a series of 5 different tests was conducted to explore the animals' search behaviour and, specifically, how well they had learned the location of the reward in the presence and absence of the landmarks.

Tests with landmarks : These took place on days 18, 19, 21 and 22. They were numbered in logical rather than chronological order. Tests 1 - 3: These were tests with both L+ and L- landmarks to establish whether the animals discriminated between the landmarks and whether they had learned the spatial locations of the food relative to the landmarks and/or relative to the arena. The F+ and F- feeders were absent until the test ended after 60 sec, at which point the F+ feeder was placed in the appropriate location and the animal allowed to eat. The positions of L+ and L- were always the same for both the Fixed and Varied groups. In Test 1 (day 18), the

landmarks were in the same positions as they had occupied during training for group Fixed (ie. Fig 5.1.); for Test 2 (day 19), the landmarks were displaced a small distance (20 cm along each axis) from this same training location; and, for Test 3 (day 22), the displacement of the landmarks relative to this training location was large (20 cm east-west and 120 cm north-south). We reasoned that the landmarks must be determining search location if the search pattern was seen to be displaced equivalently. This may prove to be easier with a small landmark displacement, for which the position of L+ within the arena would appear to the animals to have hardly changed, than it would with the larger displacement. Test 4 (day 21) was a test with identical copies of the L+ landmark placed in the same locations as during training in group Fixed. It provided an additional control for spurious cues. The white curtain was replaced by a black curtain, as the presence of the polarising cue would have disambiguated the two landmark locations in group Fixed.

Tests without landmarks : In Test NL (for No Landmarks), both the landmarks and the feeders were absent, this being procedurally identical to the nonrewarded trials conducted throughout training. This test served to indicate whether the animals were using context cues to identify the feeder location. We noticed that, in the absence of the landmarks, the animals only moved slowly away from the starting position, resulting in a bias towards the area in the immediate vicinity. To counterbalance for this, we decided to consider Test NL as the average of the performance on day 20 with that seen on day 13 using an opposite starting location (both days were during the period of asymptotic performance).

*Data collection and analyses:* Acquisition. Latency was recorded as the time taken by the animal from being placed into the arena until it found the food at F+. Latencies were averaged across trials in 2-day blocks (8 rewarded trials).

Proportion of correct first choices: An animal was considered to have made a "correct choice" if it found F+ without first checking F-. These were also averaged across trials in 2-day blocks.

*Tests* In addition to a display of the paths taken on individual trials, the software included a facility for computing the times spent searching in circumscribed areas of the arena. Several different measures were computed to examine discrimination learning and spatial learning. The first step was to measure the times spent in 20 cm x 20 cm squares, hereafter called "cells", arranged in the 11 x 11 grid centred within the arena (defined in Fig 4.2.). Of these 121 cells, we focused upon the time spent in 23 cells around L+ and 23 around L- (2 cells of the 5 x 5 grid around each landmark

being left out because of overlap of these two grid areas in some tests).

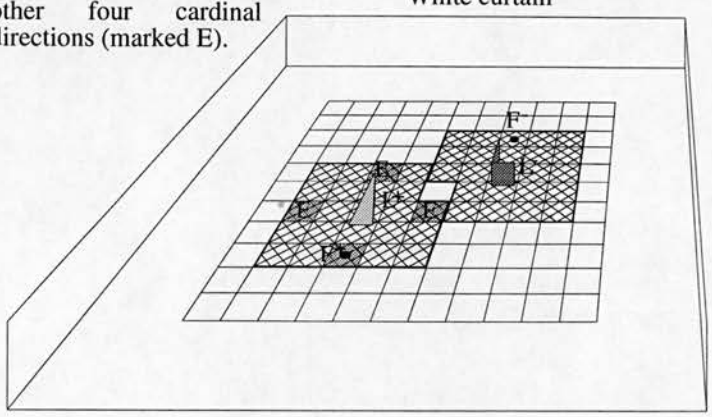



Figure 4.2. The distribution of time was recorded in an 11 x 11 grid of 20 cm x 20 cm cells. Areas A+ and A- are crosshatched. Spatial bias compared time at F+ with those in three cells at the same distasnce, but in the other four cardinal directions (marked E).

Discrimination Learning : The total time spent in the 23 cells around L+ (called A+, because it was the rewarded area) was compared to the total time spent in the corresponding area around L- (ie. A-). These times were calculated for all tests, but data from Tests 1 - 3 were averaged. In Test NL, the A+ and A- locations in both groups were as defined for group Fixed had the landmarks been present.

Spatial Learning : We computed 3 separate measures of spatial learning. The first was Time at F+. The second, called Spatial bias, involved comparing the time spent at F+ with the times spent in the 3 cells having equivalent (E) spatial relations to L+, ie. 40 cm to the north, east or west (the E cells in Fig 1A). These times were entered into a ratio of the form (A/A+B), where A was the time at F+ and B the sum of times at the other locations (chance = 0.25). The third measure, relevant only to Test 2 with the small landmark displacement, is the ratio (A/A+B) of time spent by group Fixed at F+ compared to the time at the adjacent location which F+ had occupied during training (chance = 0.5). This shows whether search shifted with the landmark in that test. As both ratio measures are undefined in rare instances when both A and B are zero, the ratio was assumed to be at chance in such cases.

## Results

The presentation of results is split into three parts. First, following a brief qualitative description of the behaviour of the animals in the arena, we outline the choice and latency data during acquisition. Second, the search patterns during the transfer tests are described qualitatively. Third, a detailed statistical analysis of these search patterns is presented. Though based on the same raw data, it is more extensive than the analysis in Biegler and Morris (1993) and modified to take account of comments.

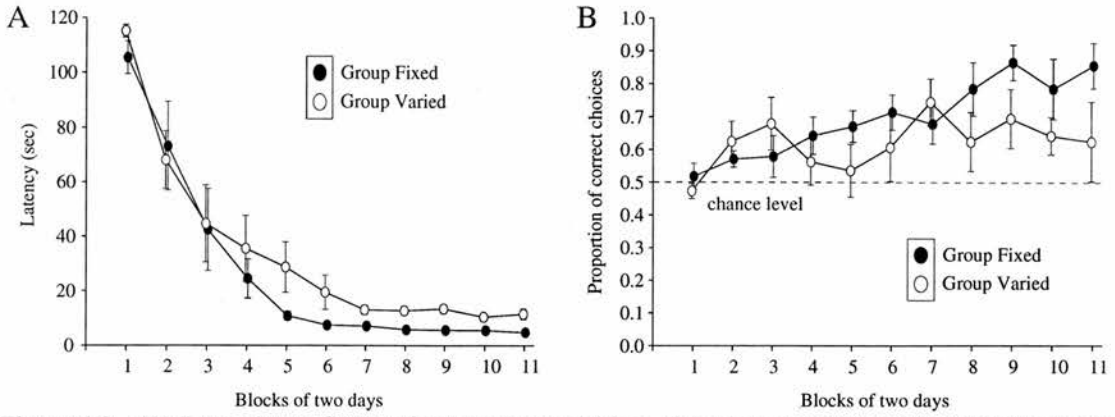



Figure 4.3. (A) Latencies to finding food during acqisition. (B) The proportion of first choices to F+ rather than F-.

*Acquisition*

Despite habituation, the rats were initially reluctant to leave the walls of the arena and often remained in the corners for long periods. When they did venture into the centre, they usually investigated the landmarks. Next came a phase marked by frequent visits to both landmarks and search in their near vicinity. As the number of visits to landmarks declined, a difference between groups became apparent. Animals in group Fixed developed a tendency to take more direct paths to the goal (F+) than those in group Varied.

There was a decline in latency ($F\ 10/120 = 60.05$, $p < 0.0001$) and an increase in the number of correct choices ($F\ 10/120 = 4.66$, $p < 0.0001$) across blocks, but no overall difference between groups on either measure (ps > 0.2; Fig 4.3.). Analysis of the choice data showed a significant Groups x Blocks interaction ($F\ 1/10 = 2.03$, $p < 0.05$).

*Tests - Qualitative description*

Fig 4.4. shows the paths taken by the animals as they moved around the arena during Tests 1, 2 and NL. There was a striking difference in the search pattern when the landmarks were absent (Test NL) compared to when they were present. During Test NL, neither group searched predominantly in the central area of the arena, nor did group Fixed search in the vicinity of F+. This indicates that the "context" cues, on their own, had little if any control over search behaviour. In Test 1, by comparison, the animals moved to the central area of the arena and spent virtually all of their time searching at or around the landmarks.

The search patterns shown in Test 1 also reveal that both groups spent more time in the vicinity of L+ than in the vicinity of L-. That is, although both landmarks were present on all training trials on which food was available, the animals discriminated

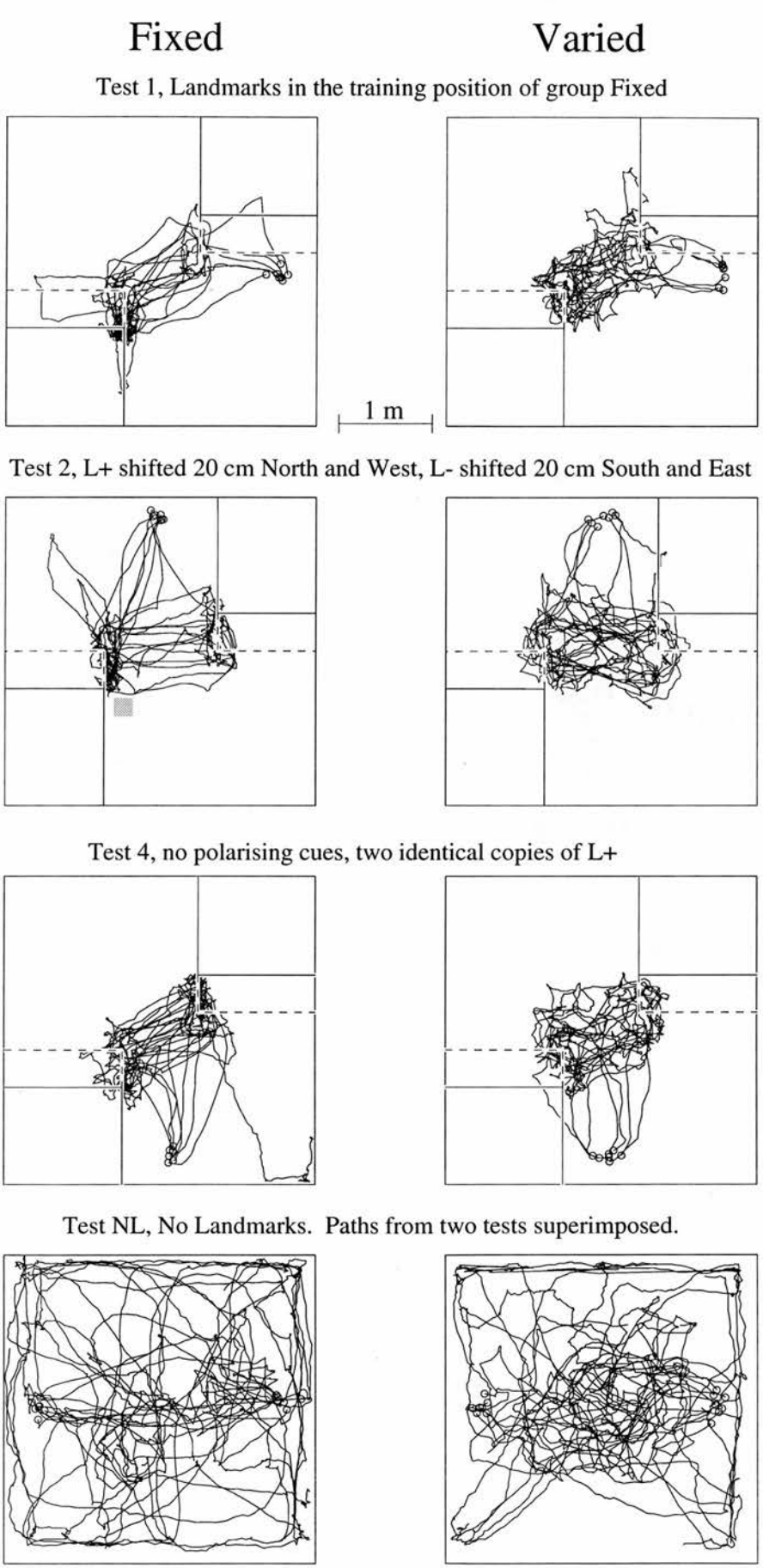



Figure 4.4. Paths during transfer tests. All diagrams have been rotated so that the white curtain is up in this figure. The small grey squares in Test 2 show the location of F+ during training and after the landmark shift. Rats did not search at the training location.

between them based on their relative proximity to F+ and F-.

There is, however, a further difference. Group Fixed spent a lot of time at F+, indeed it is the longest time in any cell. In comparison, group Varied spent most time around the L+ landmark, with no visible concentration of search at F+. This striking difference in the search pattern of the two groups suggests that spatial learning occurred only in group Fixed, while both groups learned to discriminate the landmarks.

In Test 2, with a small displacement of the landmarks, group Fixed searched at the location now specified by L+ in preference to where the feeder had been located during training. This reveals that accurate search was directed by the landmarks and not merely triggered by them. However, during Test 2, the rats spent less time searching at F+ than during Test 1, indicating that they had detected the small displacement of L+. In Test 3, with a large displacement, performance in group Fixed deteriorated further. In Test 4, using two identical L+ landmarks and no polarising cues, discrimination fell to chance in both groups.

*Tests - Quantitative analysis*

During transfer tests, search became more diffuse over time. Of the total time at F+ and the equivalent (E) locations around L+, 63.8 ± 3.7% occurred during the first 30 sec of the 60 sec tests with landmarks (Tests 1-4 inclusive). It therefore seemed most appropriate to focus on the first half of each transfer test because it gives a more accurate picture of performance.

*Discrimination learning*

Varying the landmark location across trials did not affect discrimination learning (Fig 4.5). In Tests 1 - 3, the discrimination between landmarks, defined as the difference in search time in A+ and A- respectively, was highly reliable (averaged

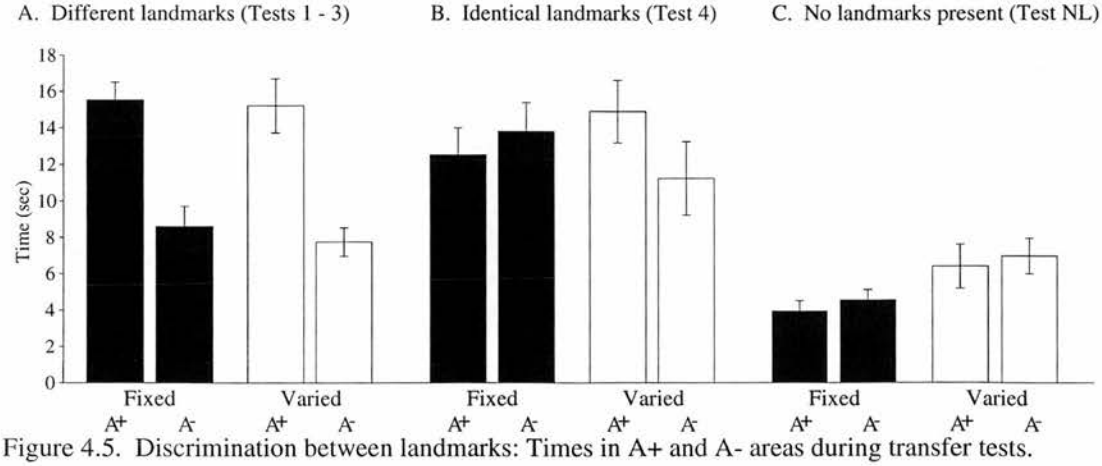


Figure 4.5. Discrimination between landmarks: Times in A+ and A- areas during transfer tests.

across tests, F 1/12 = 22.23, $p < 0.001$) with groups Fixed and Varied discriminating equally well ($F < 1$, $p > 0.8$; Fig 4.5). In Test 4, using identical landmarks and no polarising cue, discrimination fell to chance as expected ($F < 1$; Fig 4.5B). The two groups did not differ in this respect (F 1/12 = 1.16, $p > 0.3$). In Test NL, neither group showed a preference for the A+ area over the A- area ($F < 1$; Fig 5C), but the overall time spent at both areas was slightly less in group Fixed (F 1/12 = 10.90, $p < 0.02$). Note that the A+ and A- areas are of no special significance to group Varied in the absence of landmarks.

Thus, when present, the landmarks controlled discrimination performance. In tests without landmarks, the rats of group Fixed did not search in any one location and did not discriminate between landmark locations, indicating that the context cues on their own did not guide search behaviour. Paradoxically, group Varied appears to rely to a small extent on context cues to search the central area in which food could have been hidden, although this area is, in principle, predicted less accurately by the context cues than the single location in group Fixed.

*Spatial Learning*

Varying the landmark location did, however, disrupt spatial learning completely (Fig 4.6.). Group Fixed spent significantly more time at the F+ location (F 1/12 = 19.77, $p < 0.001$) and its spatial bias was more pronounced (F 1/12 = 33.97, $p < 0.0001$).

With respect to Time at F+ (Fig 4.6.), the overall difference between tests was significant (F 3/36 = 10.88, $p < 0.0001$) due to more time being spent at the feeder location in Test 1 than in any other test (ps < 0.01). A significant Groups x Test interaction (F 3/36 = 15.28, $p < 0.0001$) was caused by group Fixed spending more time at F+ than group Varied only in Test 1 ($p < 0.001$) and by a decline in the time

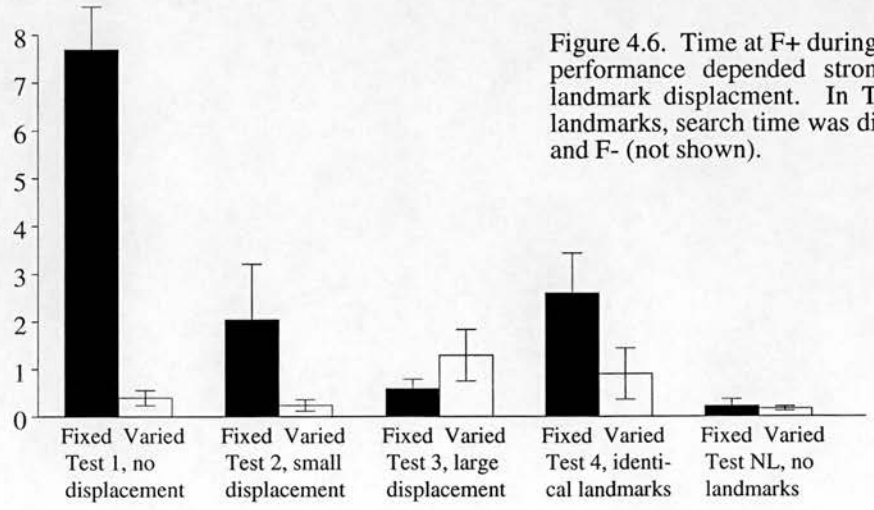



Figure 4.6. Time at F+ during tests. In group fixed performance depended strongly on the size of landmark displacment. In Test 4, with identical landmarks, search time was distributed between F+ and F- (not shown).

spent at F+ across tests by group Fixed ($p < 0.001$). In Test NL, the search distribution was far more diffuse. The maximum average time in any of the analysed 121 cells (ie. the largest pixel shown in Fig 3) was 0.39 sec for group Fixed and 0.54 sec for group Varied, compared to 7.71 sec (at F+) and 2.57 sec (near the L+ landmark) respectively in Test 1. However, the critical measure, in assessing the control of search by context cues in the absence of the landmarks, is the time spent at F+. In Test NL, this was 0.22 + 0.14 sec for group Fixed and 0.16 + 0.05 for group Varied. Neither differed from the chance level of 0.11 sec ($t< 1$; $t=1.18$; $ps > 0.10$, respectively).

With respect to Spatial bias (Fig 4.7.), Group Fixed performed above chance in all four tests with landmarks, group Varied in none. The difference between the groups was significant ($F\ 1/36 = 33.97$, $p < 0.0001$). There was no effect of Tests ($F < 1$), nor a Groups x Test interaction ($F\ 3/36 = 1.72$, $p > 0.1$). The similar scores for spatial bias in Test 4 (identical landmarks) were to be expected as the spatial relations between the two L+ landmarks and their respective F+ locations remained unchanged.

Test 2, with a small landmark displacement, was conducted to investigate whether search for F+ would occur at the location specified by the now shifted L+ or at that defined by context cues (Fig 4.4.). Six of seven rats searched at the former location, none at the latter, giving a ratio of search at these two locations of $0.93 \pm 0.07$, well above chance ($p < 0.0001$). It should be noted that this concentration of search at the F+ location specified by the shifted landmark occurred despite the animals having detected that the landmark had moved (see above).

## Discussion

The main findings of Experiment 1 were: (1) the dissociation between spatial and discrimination learning, and (2) that landmark stability affected spatial learning. Both

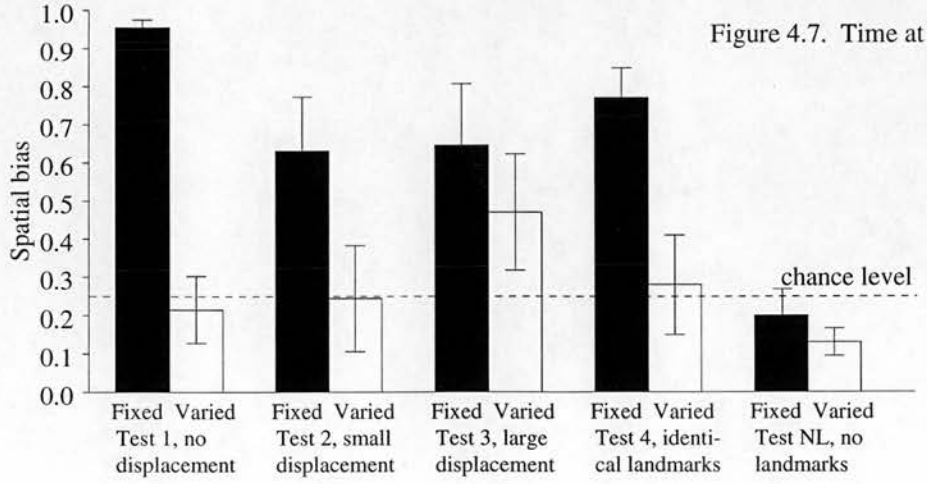



Figure 4.7. Time at F+ during tests.

groups searched preferentially around the L+ rather than the L- landmark, discriminating equally well between the landmarks with respect to their proximity to the accessible food. However, only the group with the landmarks in fixed locations learned their relation to food. Group Fixed spent far more time searching at the F+ location during Test 1 with the landmarks present than in Test NL when they were absent; it also showed a clear Spatial bias to F+ rather than any other location around the L+ landmark. Group Varied spent little time searching at F+ and showed no spatial bias. The greater time at F+ in group Fixed cannot have been due to context cues because time at F+ in the absence of the landmarks was very low and did not differ from chance. If anything, the contribution of context cues to search in the central area of the arena was greater in group Varied.

It was intended that the groups should only differ in the accuracy of distance information available from landmark or context cues. Under this assumption the effect of landmark stability is surprising from the perspective of associative learning theory. Learning about the relationship between discrete cues (such as lights or tones) and the events they may predict (such as food), proceeds most effectively under conditions in which a cue is the sole predictor of reward. In this experiment the probability of receiving food was the same for both groups, but in group Fixed use of the walls and curtains could restrict search to a much smaller area than in group Varied. Therefore control by the landmark should have been best in group Varied, yet search was most focused during Test 1 in group Fixed. This result could be explained in associative terms if that focused search was an additive effect of both context cues and landmark. But the random search in the absence of landmarks establishes that this was not the case. An alternative associative explanation is that the landmarks were mere conditional signals, or occasion setters, triggering search at the F+ location as defined by context cues. This is ruled out by the results of Test 2, in which the location of search was determined by the displaced location of L+. It follows that the better learning of the landmark/F+ spatial relationship by group Fixed cannot be explained by competition between landmark and context cues for a limited sum of associative strength or attention. Such additive interaction is assumed to be the basis of contingency effects, overshadowing and blocking in conditioning. Instead the results may be interpreted in terms of a principle of landmark stability: "If it moves, don't use it as a landmark". The assumption is that navigational processes evolved to build a stable representation of the world, and if an object moves, there is no reason to assume that other items of interest will move with it. Therefore it should

be ignored. Obviously, there must be a limit below which movement has no effect, even if it is only a limit of detecting movement. If the decision is not an all-or-nothing process, the rule may be similar to that found when creating a discrepancy between sources of spatial information after training in a stable environment: Classify information according to accuracy and reliability. When there is a discrepancy, give relatively less weight to unreliable information the larger that discrepancy is. This would a multiplicative, rather than additive interaction.

There are two factors limiting the necessity to appeal to a principle of landmark stability in this experiment. First, it was intended that the only difference between groups should be in landmark displacement, not in directional cues. However, after publication of these data (Biegler and Morris 1993), we realised that the consistently asymmetric placement of L+ and its stable relationship to L- may have given group Fixed directional cues not available to group Varied. If distance and direction from landmarks were learned independently, this would make no difference. If there was no landmark stability effect, group Varied would still be expected to search at least at the right distance from L+. On the other hand, if it is only possible to represent complete landmark goal vectors, with both distance and direction or distances in two axes, lack of a good directional cue would mean group Varied simply had no spatial relationship available that it could learn.

Second, an account within the framework of associative learning theory may be possible if it is assumed that spatial representation requires configural associations (Sutherland & Rudy, 1989). In each landmark location in the arena, the view of the L+ landmark from the goal would form a unique configuration with background cues. Slower learning by group Varied would follow because it would need to learn as many different configurations as there are landmark locations. The contextual retrieval hypothesis (Hall & Honey, 1989) gives a similar account, with neither being concerned with the spatial arrangement of the landmarks in an array. Altering the spatial arrangement of landmarks across groups would not change the number of configural associations to be formed, and so have no effect on rate of learning. In contrast, an interpretation of cognitive mapping that allows the formation of small-scale local maps (O'Keefe, 1991; Worden, 1992) would regard such a parameter as critical. A directional cue, a single landmark and a feeder only specify two spatial variables. A triangular array of two separate landmarks and a feeder has at least six variables, three angles and three distances. A directional cue will add three angles. Local stability of these variables may be sufficient to support spatial learning even in

the absence of global stability relative to a larger frame of reference.

In summary, a simple associative theory incorrectly predicts that landmark stability should reduce the strength of the association between the landmark and reward through competition by other cues. A configural or context-retrieval hypothesis may be able to explain the results od Experiment 1, but predicts that rate of learning would be independent of the spatial arrangement of landmarks. The availability of directional cues must not be confounded with landmark stability. The next experiment was designed to address the issues of directional cues and local versus global landmark stability.

## 4.2. Experiment 2: Local and global stability

In Experiment 2 the L+ landmark or array was placed in the centre of the arena (on average) to avoid giving a directional cue through asymmetric placement. This was only an average placement, as in group Varied the landmark had to move. To avoid accumulation of olfactory traces in one spot, the landmark or array also moved in group "Fixed", but the size of displacement was smaller by a factor 5. No L- landmark was used to remove any effect of its relationship with L+. Arrays of a "Single" landmark and feeder were compared with triangular "Spaced" arrays of two landmarks and feeder. To control for possible effects of greater salience of two landmarks there was a third "Clustered" landmark arrangement, where the two landmarks were as close side by side as physically possible.

### Methods

Subjects The subjects were 42 experimentally naive male Lister-hooded rats, maintained at 85% of their free feeding weight. These were selected from a total of 64 animals run until the second day of training. The rats continuing the experiment were those that searched reliably for food. Animals were assigned at random to groups before this selection was made.

*Apparatus* The experiment was conducted in the same apparatus as Experiment 1. The only changes were the use of "Kellogg's Ricicles" as reward (which are the same colour as the sawdust) and the presence of a loudspeaker behind the centre of each wall. During training the speaker to the "north" (behind the wall under the white curtain) emitted white noise to mask potential acoustic cues and to provide an additional directional cue.

There were two landmarks (Fig 4.8). L1 was a steep pyramid with a 15 cm wide base and 29.2 cm high. At 19.4 cm and 11.6 cm height were two protruding "terraces" of 2 cm and 2.5 cm width. Between the two terraces, the landmark was covered with rough sandpaper with a black stripe of 2.2 cm width below the lower terrace. The rest of the landmark was painted "signal red". Inside the tip of L1 was some carpet to which 1 ml of almond essence was added before each session. Holes in the top allowed the odour to escape. Landmark L2 consisted of a stack of four layers of four golf balls each on a wooden base, with a green tennis ball on top. The lower half of the tennis ball had 1 ml of strawberry essence added. L2 was 25.5 cm high with a maximum diameter of 9.8 cm. In a pilot study these landmarks had been shown to be easily discriminable. There were two copies of each landmark, used in

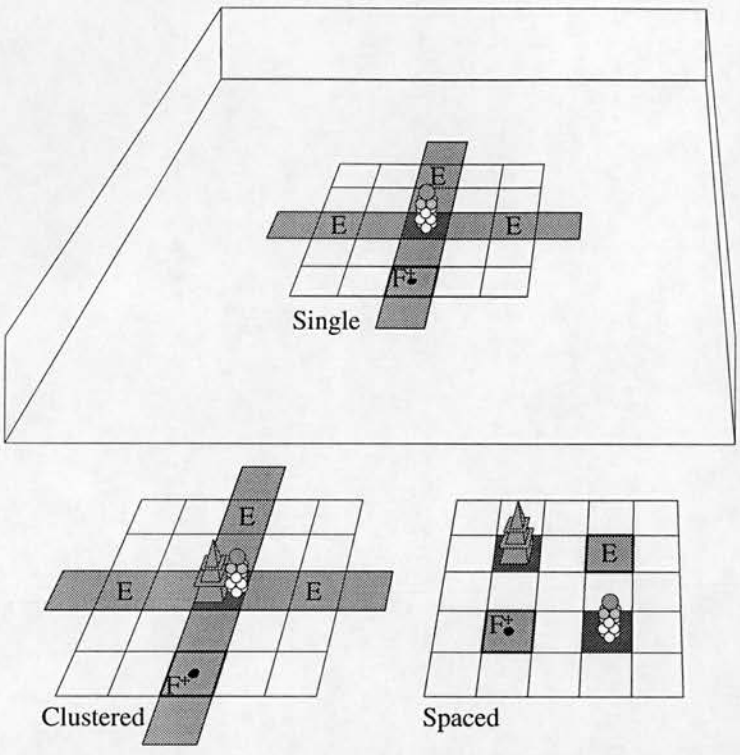






Figure 4.8. Landmark configurations, arena and areas included in the quantitative analysis. In the Single landmark configuration, the identity of the landmark was counterbalanced within groups. In Clustered and Spaced configurations the identity of the landmarks in Test 3 was counterbalanced. Time at F+ was recorded in all groups. Directional bias, compared cumulative time in the three light grey cells in the direction of F+ with the cumulative time in the corresponding cells in the three other cardinal directions. The chance level is 0.25. Distance ratio, compared the average time in the F+ and E cells with the average time in the "background" - this being defined as including all cells in a 5 x 5 grid centred on the landmark, excepting those of the landmark location itself (dark grey) and the F+ and E cells. Chance level is 0.5. The analysis of Directional bias and Distance ratio in Single and Clustered configurations is identical. In the Spaced configuration only 2 cells are at equivalent directions from both landmarks and the chance level of Directional bias is therefore 0.5.

alternation throughout training in anticipation of the test with two identical landmarks.

Only one feeder, containing accessible food, could be present during training (F+). It was placed 50 cm south of a single landmark or two landmark cluster, and 50 cm south of L1 and 50 cm west of L2 in the Spaced landmark array condition (see below and Fig 4.8.).

*Procedure* Pretraining: The rats had 10 days of handling and training to eat from the feeder in a separate cage in the animal house. This was followed by 3 days of habituation in the maze. During the first 2 days, they spent 2 half hour sessions per day in the empty arena, in groups of 4 rats. On the third day of habituation, individual animals had one 10 min habituation session during which 4 feeders were in the arena, arranged in a square of 1m each side. We recorded which feeder was visited first and the latency until the correct feeder was found.

Training: Training conditions differed along two independent dimensions: Landmark Stability and Landmark Arrangement. In the Stability dimension, groups were again divided into Fixed and Varied. For the Varied groups, the landmarks were moved randomly between 15 possible locations in a 4 x 4 grid with 50 cm spacing (ie. around a 1.5 m x 1.5 m area within the 3.3 m x 3.3 m arena; Fig 4.9). For the Fixed

groups, the landmarks were not literally immobile, but moved in a similar grid with 10 cm spacing between adjacent positions (ie a 30 cm x 30 cm area; Fig 4.9). In the other dimension, groups were trained with one of three landmark arrangements - Single, Clustered and Spaced. The Single arrangement consisted of only one landmark 50 cm north of F+, Clustered of two landmarks side by side replacing the one landmark of the Single arrangement, and the Spaced arrangement of landmarks and feeder forming a right-angled triangle with both landmarks 50 cm from the feeder (Fig 4.8). For a given trial, the landmark(s) were placed on the target position of the grid for groups Single and Clustered, and the centre of the landmark array for group Spaced. Thus, there were six groups: Fixed-Single (example in Figure 4.9), Varied-Single, Fixed-Clustered, Varied-Clustered (Fig 4.9), Fixed-Spaced, and Varied-Spaced (Fig 4.9; N=7 for all groups).

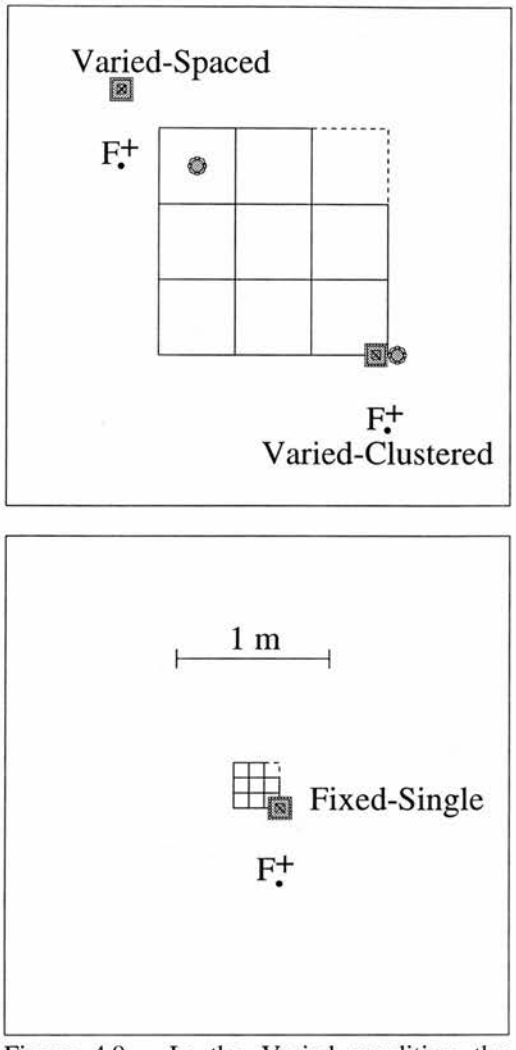



Figure 4.9. In the Varied condition the location of the array varied rasndomly between 15 positions in a 4 x 4 grid with 50 cm spacing. The 16th position, indicated by dashed lines, was used only in a test. In the fixed condition the array moved between the corresponding positions in a grid with 10 cm spacing. In Single and Clustered arrangments, the landmarks were placed directly on grid positions, in the Spaced arrangement the centre of the landmark array.

The landmarks and feeder were introduced on the first day of training. The array of landmarks and feeder was moved before each trial, in a random sequence, to a different grid position, with the constraint that the array was not in one of the two positions closest to the start location. The orientation of the polarising cues and arrays was changed between trials in a random sequence.

Training protocol: The subjects were again transported to the start locations in the opaque, slowly rotating box. They started a trial facing one of the walls in a random sequence, with the constraint that each of the 4 start positions was used once a day. They were run in groups of 6 - 8 animals, so the ITI for each particular rat depended on the latency of the others. ITI varied from about 80 min at the beginning of training

to about 60 min at the end.

The rats were trained for 25 days. During the first two days there were 2 trials per day, both rewarded, on all other days 4 trials, 1 of them unrewarded. A training trial ended when the rat found the food or after 300 sec, whichever was the shorter. A rat which failed to find the food within 300 sec was picked up and placed in front of the feeder until it ate. The feeder was then refilled and the bedding thoroughly shuffled before the next rat was put in the maze. During the first 5 days, the top of the feeder was 2 - 3 cm above the bedding. On days 6 to 8, this margin was reduced to about 1 cm. On all subsequent days the bedding was level with the feeder. Rats were removed from the maze before they stopped eating. The unrewarded trial of 60 sec duration, in which neither food nor landmarks were present, was intermixed with normal training trials.

Transfer tests: There were four types of test, all of 60 sec duration. Test 1 (day 21), was conducted with polarising cues and with the landmark array in a position previously used in training (familiar location). At that point in training, there had been exactly 60 rewarded trials, with 4 in each of the 15 positions used in training. In Test 2 (day 23), the landmark array was in a novel position, the 16th location of the grids not used during training. Test 3 (day 25) was conducted without polarising cues. There were black curtains on all sides, all four speakers emitted noise, and two identical landmarks were used for the Spaced and Clustered groups (L1 and L2 were counterbalanced within groups). Test NL (no landmarks) was the average of 3 tests on days 20, 22 and 24.

*Data collection and analyses* The image analyser was replaced by a digitising board that performed video frame grabbing at 10Hz; this gave better tracking of the animals (Spooner et al., 1994). Otherwise, data collection proceeded as in Experiment 1.

Acquisition. Latencies: These were averaged across trials in 2-day blocks. As there was an odd number of training days, day 25 was excluded from the analysis.

Transfer tests. Search distribution was computed for 29 cells around the landmarks, 25 in a 5 x 5 grid whose centre coincided with those of the respective landmark arrays, plus 1 cell beyond this grid in each of the four cardinal directions. Each cell measured 25 cm x 25 cm. Three measures of performance were calculated.

First, Time at F+ provides a measure of commitment to search at the correct location, but confounds knowledge of direction and distance. These two components were assessed separately in the two other measures.

Second, Directional bias, which took the form A/(A + B), was calculated for the Single and Clustered conditions by comparing total time spent in the three cells in the direction of F+ (ie. F+ itself and the cells closer to and further from the landmark; area A) with the sum of times spent in the corresponding cells in the other three cardinal directions (area B). The chance level is 0.25. Directional bias may be less sensitive than Spatial bias used in Experiment 1, as it includes some of the time the animals spend walking round the landmark, but has the advantage of being independent from distance (Spatial bias reflects knowledge of direction at the correct distance only. It was used in Experiment 1 because the landmarks extended into cells adjacent to the central one and, in some tests, the landmarks were sufficiently close together that search at L- could have influenced directional bias at L+. In Experiments 2 and 3, these constraints no longer applied). In the Spaced landmarks condition, only two cells are at equivalent directions from both landmarks (F+ and E in Fig 7A). Therefore, in calculating Directional Bias using the ratio A/(A + B), A was taken as the time at F+ and B as the time at the opposite location (E). Consequently, the chance level changes to 0.5 and so parametric statistical comparisons with Single and Clustered arrangements are not possible.

Third, Distance ratio was an analogous A/(A+B) ratio, where A was the average of time at F+ and at the equivalent locations (E in Fig 4.9.) and B the average time in the "background". The background consisted of all locations in a 5 x 5 grid of 25 cm x 25 cm cells around the landmark, excepting cells containing landmarks, F+ or E locations. Chance levels are equal in all groups (0.5) and parametric statistics can be used.

## Results

*Acquisition*

Although initially reluctant to leave the walls, only 3 rats (out of 42) failed to find reward unaided during the first trial (day 1). Performance improved steadily before (blocks 1-4) and after (blocks 5-12) the feeder was flush with the surface (Fig 4.10). Systematic search patterns appeared within a few days in groups Fixed-Single and Fixed-Clustered. Most frequently, the rats of these groups would check a location at the correct distance from the landmark(s), return to the landmark(s) and then turn and visit the next location until finding food at the correct place. Such patterns were much less frequent in the Varied-Single and Varied-Clustered groups for which the animals adopted apparently random searching near the landmark(s). In the Spaced-landmarks groups, preferential searching on the appropriate side of the 2 landmarks

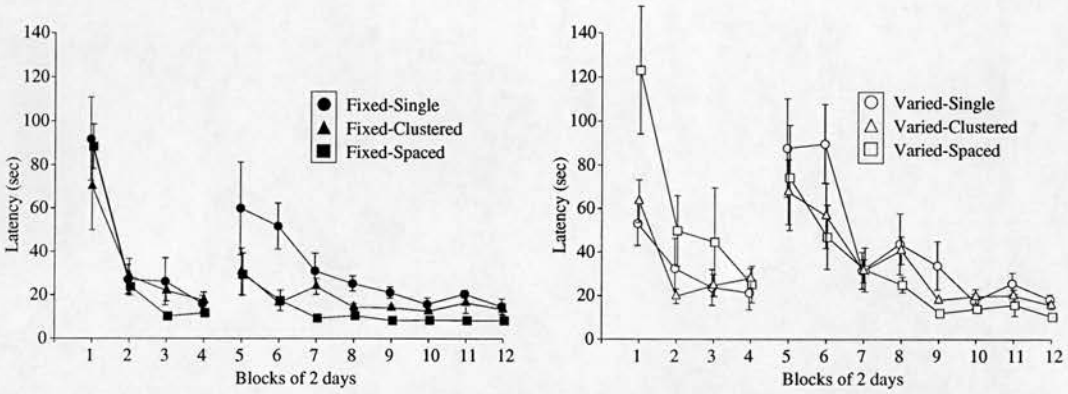



Figure 4.10. Latency to find food (sec ±1 S.E.M.) during training with a visible feeder (blocks 1-4) and with a hidden feeder (blocks 5-12). Note faster times to find food in groups with two landmarks during the early stages of training with a hidden feeder.

emerged relatively early with the accuracy improving during training. Visits to the symmetric location opposite to the feeder occurred only rarely.

While the feeder was visible, analysis of latencies showed neither an effect of Arrangement nor Stability (Fs < 1). The improvement across Blocks was highly significant ($F\ 3/108 = 84.19$, $p < 0.0001$) as was the Arrangement x Blocks interaction ($F\ 6/108 = 3.51$, $p < 0.01$). Differences between arrangements existed only during the first block, when the Spaced-landmarks groups' latencies were longer.

When the feeder was hidden, effects of Arrangement ($F\ 2/36 = 6.44$, $p < 0.005$) and Stability ($F\ 1/36 = 16.54$, $p < 0.001$) appeared. Single landmark groups had longer latencies than Clustered and Spaced groups ($p < 0.05$, t-test) and Varied groups took longer than Fixed groups. The rats improved over blocks ($F\ 7/252 = 24.70$, $p < 0.0001$), with a Stability x Block interaction ($F\ 7/252 = 4.53$, $p < 0.0001$). In an analysis of blocks 10-12 (ie. the transfer test days), the effects of Stability ($F\ 1/36 = 7.39$, $p < 0.01$) and Arrangement ($F\ 2/36 = 8.96$, $p < 0.001$) were still significant, but the Spaced groups had lower latencies ($p < 0.01$, t-test) than either Single or Clustered groups, which in turn did not differ from each other. Thus, search latency with a hidden feeder appeared to be influenced by the number of landmarks early in training, and by their spatial arrangement later on.

*Tests - Qualitative description*

The paths taken by all rats during Tests 1 and 2 are shown in Fig 4.11. Three qualitative features of the paths are apparent: First, the most focused searching at the correct F+ location was in the Fixed-Spaced group (Fig 4.11, bottom-left), although, even in this group, search accuracy was much lower than in Experiment 1. Second, the Fixed-Single and Fixed-Clustered groups showed no obvious directional preference relative to the polarising cues, but focused their search at the appropriate

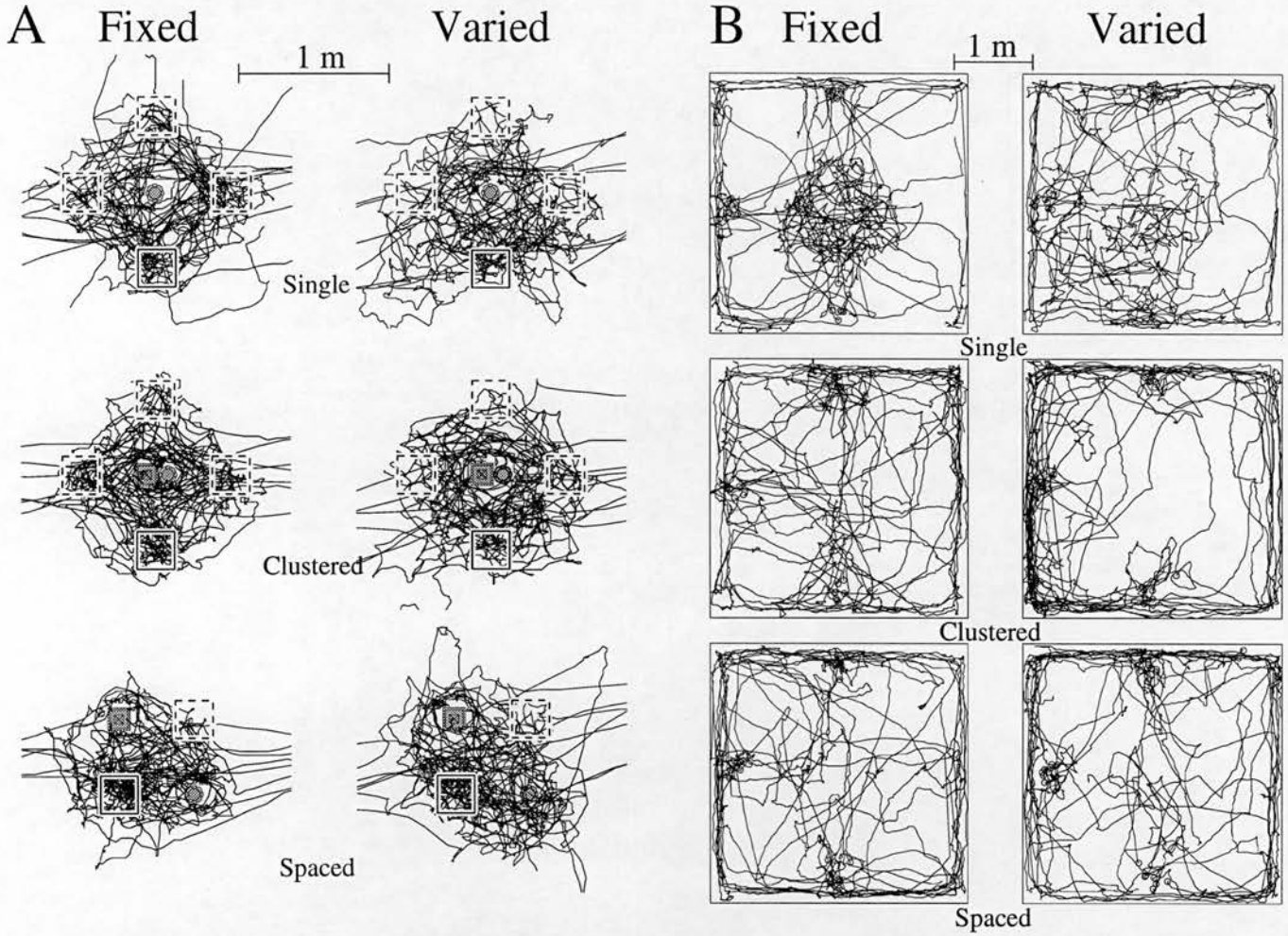



Figure 4.11. (A) Superimposed paths of all rats during the first 30 secs of Tests 1 and 2, with familiar and novel landmark locations. Only the area immediately surrounding the landmarks is shown. The cell where F+ was placed during training is marked by a square. Other cells at equivalent distance and directions (relative to the walls of the maze) are marked by broken squares. The cells measure 25 cm across. Scale bar = 1 metre. (B) Paths taken during three tests with no landmarks. Rats in all groups spent a large proportion of time near the walls. Note change of scale from panel A.

distance and direction relative to the walls (the geometry of the arena defines 4 equivalent locations). Third, the Varied-Single and Varied-Clustered groups searched with a more diffuse pattern and closer to the landmark(s). The paths taken during the three tests without landmarks (constituting Test NL) are shown in Fig 4.11B. All animals spent a great deal of time near the side walls. Other than in group Fixed-Single, there is relatively little searching in the general area of the arena where food might have been found. The quantitative analysis bears out this qualitative description.

*Tests - Quantitative analysis*

There are two preliminary considerations. First, it was decided to base the analysis on only the first half of each transfer test. The reason is that, as in Experiment 1, search was more focused at the appropriate distance during the first half of the 60 sec tests; averaged across all groups and tests, 61.6 ± 2.1% of search at the F+ and E locations occurred during the first 30 sec. Second, we treated the landmark cluster (2 landmarks side-by-side) as if it were a single landmark defining four, not two, equivalent directions. The reason is that, had the animals used the axis of symmetry of the 2 clustered landmarks, they would have been expected, in Test 3 (without polarisation and with identical landmarks), to have spent more time at the F+ and opposite locations than at the E locations to the right or left of the landmark cluster. The proportion was 0.43 ± 0.07 - no different from chance. That is, the animals ignored the breaking of the maze's fourfold symmetry by the single symmetry axis of the landmark cluster and it can therefore be treated as if it were a single landmark.

Time at F+ : With the landmarks present, the animals spent virtually all of the first 30 sec of each test searching near them. Groups Fixed-Spaced and Varied-Spaced spent the most time at F+, 5.4 + 0.9 and 3.7 + 0.5 sec respectively. An analysis of Tests 1 and 2 revealed that Fixed groups spent more time at F+ than Varied groups ($F\ 1/36 = 5.90$, $p < 0.05$) and that there was a significant effect of Landmark Arrangement ($F\ 2/36 = 8.18$, $p < 0.005$). A subsequent analysis of the effect of Arrangement revealed that the Spaced landmark groups spent more time at F+ than the mean of the Single and Clustered groups ($F\ 1/36 = 16.12$, $p < 0.001$) which, in turn, did not differ from each other ($F < 1$). There was no difference in the performance during Test 1 (F+ in one of the training locations) from that in Test 2 (F+ in a 16th novel position) and, for simplicity, the results of these two tests have therefore been averaged in Fig 4.12. Time at F+ is influenced by both landmark

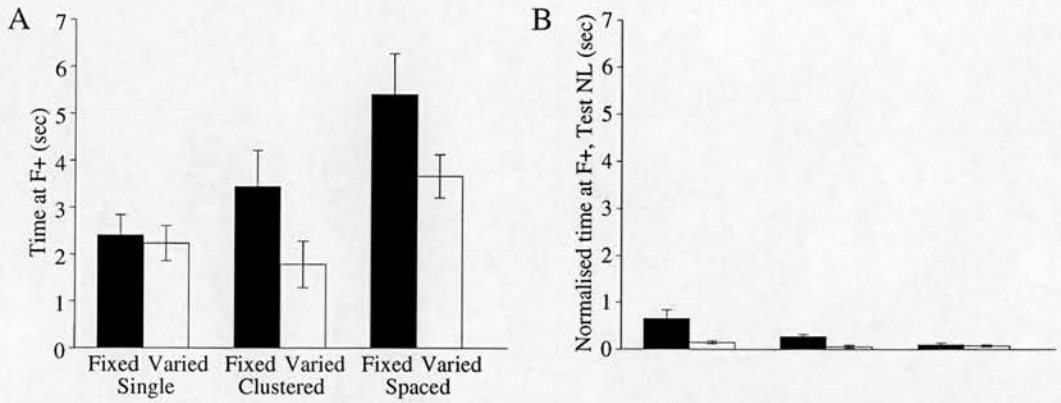


Figure 4.12. (A) Time at F+ (sec ±1 S.E.M.). Data are averaged across Tests 1 and 2. (B) Normalised Time at F+ (No landmarks) plotted to same scale as A.

stability and landmark arrangement.

Normalised Time at F+ (No landmarks): An important step in the analysis is to establish the relative degree of control over searching by the context cues and by the landmark(s). Fig 4.12B shows the Normalised Time at F+ (No landmarks) for all groups to the same scale as in Fig 4.12A. A key point is that the absolute values of these times are very low, never exceeding 0.65 sec per square. In addition, the scores for the two Spaced groups - 0.10 + 0.04 and 0.08 + 0.02 sec - were 1.5 orders of magnitude lower than those for Time at F+ in Tests 1 and 2 (see above). An analysis of variance did, however, show effects of Stability ($F\ 1/36 = 13.42$, $p < 0.001$), Arrangement ($F\ 2/36 = 6.98$, $p < 0.005$) and a Stability x Arrangement interaction ($F\ 2/36 = 4.82$, $p < 0.025$). The pattern giving rise to this interaction was different from what was observed with the landmarks present. Significantly greater searching was found in the groups with one landmark than in those with two landmarks, and analysis of the interaction showed this difference was only apparent in groups Fixed ($p < 0.001$). The Clustered and Spaced groups did not differ ($p > 0.05$). Likewise, the effect of landmark stability occurred only in the single landmark groups, with greater control by context cues in group Fixed-Single than group Varied-Single ($p < 0.001$). Control over searching by context cues alone depended on stability and the number of landmarks rather than their arrangement.

Directional bias : Fig 4.13A shows the directional bias averaged across Tests 1 and 2, together with the chance level of performance which was 0.25 for the Single and Clustered groups and 0.5 for the Spaced groups (see Methods). The analysis of the Single and Clustered groups showed no significant difference between the Fixed and Varied groups (Stability $F\ 1/24 = 3.05$, $p = 0.094$), no difference between Single and Clustered Arrangements ($F < 1$), and no Stability x Arrangement interaction ($F\ 1/$

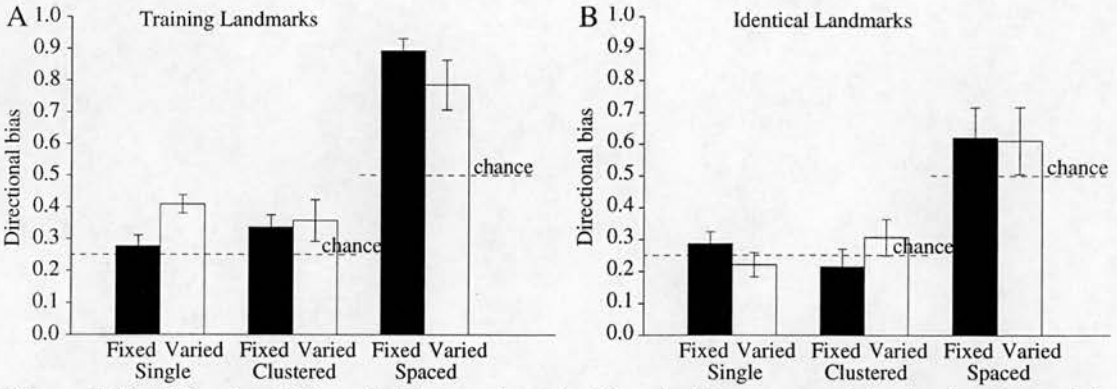



Figure 4.13. Directional bias. A) Test conducted with polarising cues and the landmarks used in training. Data are averaged across Tests 1 and 2. (B) Test with identical landmarks but without polarising cues. ±1 S.E.M.

24 = 1.59, $p > 0.2$). However, the above chance performance of group Varied-Single was unexpected (0.41 + 0.03, t=5.48, $p < 0.001$). Examination of the paths revealed that this group searched closer to the landmark than group Fixed-Single and that its search distribution was displaced away from the polarising cues. Displacement alone cannot account for the above-chance performance, as directional bias is insensitive to distance.

A separate analysis of the two Spaced landmark groups revealed no effect of Stability ($F\ 1/12 = 1.48$, $p > 0.20$) but, as shown in Fig 4.13A, both groups had directional bias scores that were well above chance ($ps < 0.001$). In combination with the apparent ineffectiveness of the polarising cues this seems to suggest that animals trained with a Spaced landmark array derived their reference direction from the two landmarks. Comparison with animals trained in a different experiment shows that this inference is too simple. The procedures of group Fixed-Spaced were exactly replicated up to the first test, with the exception that there were no polarising cues. Directional bias was at chance at significantly lower than in the Fixed-Spaced group of Experiment 2 ($t = 7.15$, $df = 10$, $p < 0.001$), while distance ratio was indistinguishable ($t = 0.71$, $df = 10$, $p > 0.4$). The Spaced groups in Experiment 2 may have benefited from mutual potentiation of directional information from landmark array and polarising cues (see Experiment 3).

Because directional bias is calculated in a different way for the three arrangements, we cannot compare the Spaced-landmark groups with the Single- and Clustered landmark groups. It was important to establish, however, that directional bias would fall to chance for all three landmark arrangements when the polarising cues were removed and, for two of these conditions, the landmarks were identical. This was checked in Test 3 for all groups. None of the groups differed from chance

(Fig 4.13B). Furthermore, two separate Anovas showed that the groups did not differ from each other (Fs < 1).

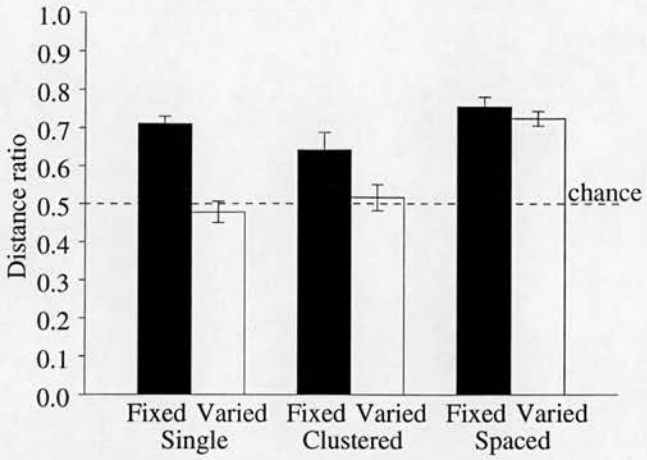



Figure 4.14. Distance ratio averaged across all tests. ± 1 S.E.M.

Distance ratio : The results described so far indicate that the polarising cues (white curtain and localised sound source) were less salient than we had anticipated. If this is true, it means that the animals had relatively little directional information except in the Spaced-landmark groups. The question therefore arises of whether distance information can still be processed effectively in the relative absence of directional information, and of how such processing is influenced by landmark stability.

Fig 4.14 shows the mean distance ratios of the 6 groups averaged across Tests 1 - 3 (Test 3 can be included because the computation of distance ratio is independent of directional information). The overall analysis revealed a highly significant effect of Stability ($F\ 1/36 = 27.15$, $p < 0.0001$), Arrangement ($F\ 2/36 = 17.13$, $p < 0.0001$) and a significant Stability x Arrangement interaction ($F\ 2/36 = 5.58$, $p < 0.01$). While the Fixed groups performed better than the Varied groups in the Single and Clustered landmark conditions (ps < 0.05), there was no such difference in the Spaced groups ($p > 0.20$). These contrasts were established using separate F tests and Scheffé's method of adjusting error-rate for multiple comparisons (Myers, 1966, p 333). A complication in this otherwise striking pattern of results is that the overall analysis also revealed a significant change in distance ratio across successive transfer tests ($F\ 2/72 = 3.46$, $p < 0.05$) and a significant triple interaction between Tests, Stability and Arrangement ($F\ 4/72 = 3.48$, $p < 0.025$; data not shown). Inspection of the data showed that the performance of group Fixed-Clustered decreased markedly from Test 1 (landmarks in a training location) to Test 2 (landmarks in a novel location). We have no explanation for this effect.

## Discussion

The main findings were: (1) the polarising context cues exerted little control over searching on their own, but an effect of relative validity was observed; (2) an effect of landmark stability was again observed - spatial learning was impaired when a

single landmark moved locations during training, and (3) the square geometry of the arena and the spatial arrangement of a pair of landmarks were both important determinants of learning.

The overall performance of the groups was poorer than in Experiment 1. Most strikingly, the Fixed-Single and Fixed-Clustered groups showed no directional bias suggesting that, in Experiment 1, the consistent spatial relationship between L+ and L- in group Fixed provided an important directional cue (compare Figs 4.4 and 4.11). It also indicates that, under the conditions used in both Experiments 1 and 2, the white curtain was not a very effective polarising cue, consistent with Cheng's (1986) and Margules and Gallistel's (1988) observations. This implies that in Experiment 1 the consistent spatial relationship between L+ and L- and/or the asymmetric placement of L+ in group Fixed probably provided an important directional cue. As group Varied did not benefit equivalently, the conclusion drawn then that landmark stability influences spatial learning would be insecure on the basis of that study alone.

Only a speculative account can be given for group Varied-Single showing directional bias. It requires the assumption that overshadowing can work on two levels, that of cues and that of 'hypotheses', as suggested by Krechevsky (1932, 1933) and later by O'Keefe and Nadel (1978). Then group Fixed-Single would not show directional bias because landmark stability allows a distance-based strategy to overshadow the weak directional cues. In group Varied-Clustered use of directional cues would be overshadowed by the greater salience of two landmarks.

In Experiment 2 context cues did have a small but significant influence on searching patterns when the landmarks were absent. As expected on the basis of associative learning theory, greater control was observed in group Fixed-Single than Varied-Single, and there was a decline in control as the number of landmarks increased, independent of their arrangement. This pattern is in accord with a principle of relative validity - context cues showing greatest (albeit rather weak) control in a situation in which the context most informative and the landmark(s) least salient. The control by context cues is insufficient to account for the much larger differences between groups observed with the landmarks present.

The significant effect of landmark stability in the groups with either a single landmark or clustered landmarks was shown in the Time at F+ measure and, most clearly, in the Distance ratio measure of Fig 4.14. The paths taken by the rats in Fixed-Single and Fixed-Clustered indicate that direction (relative to the walls) and distance (from the landmark) had been learned. That is, these two groups had learned

the geometrical arrangement between food and landmark relative to the walls of the arena. Had they learned only the appropriate distance, they would have searched around the landmark in a circle; had they learned only to walk towards or away from the landmark(s) parallel to one of the walls, not knowing at what distance to stop, they would have spent a substantial proportion of time too far away from the landmark. Neither pattern was observed. Thus, landmark stability can positively influence performance even when directional information is ambiguous or weak.

The contrast between the Single and Clustered arrangements, and the Spaced Landmark arrangement, both in overall performance and in the lack of a difference between Fixed-Spaced and Varied-Spaced, is also of interest. The pattern of results contradicts the prediction of contextual and configural associative theories that the effect of moving a landmark array should be independent of the spatial arrangement of the landmarks. It is consistent with predictions of O'Keefe's (1991) and Worden's (1992) mapping theories that local landmark stability should be sufficient to support spatial learning given a minimum of either two or three landmarks. Note, however, that if spatial relations are assumed to be elements of configural associations (Sutherland & Rudy 1989, p. 130), this theory may become equivalent to cognitive mapping theory. Processing within the configural association system is not described in sufficient detail to allow a definitive interpretation.

Finally, in group Fixed-Clustered, distance ratio decreased in the test with a novel position (Test 2). We are unable to explain this result. Had it occurred in the Varied group, such an effect would have strongly suggested that the search for food constituted a separate task for each individual landmark position. Navigation might have proceeded by matching a remembered view to the currently perceived view of the environment, with background cues and the landmark both being essential parts of this remembered view. However, not only did this decline in distance ratio not occur in the Varied groups, but, in the Fixed groups, adjacent landmark positions within the grid used in training were only 10 cm apart. There is no evidence that the rats can detect such a small displacement of the landmarks relative to walls that are 15 times as far away.

## 4.3. Experiment 3: The effects of directional cues

The primary weakness of Experiment 2 is the apparent lack of effective polarising cues for the Single and Clustered groups. These groups largely disregarded the polarising curtain and noise source and so did not have an unambiguous directional reference. In a study of hippocampal place cells and thalamic directional cells, Knierim et al. (1995) found that a disorientation procedure similar to ours made rats disregard a cue card in a small circular open field maze and frequently led to random remapping of place fields. Vestibular and visual cues had to be mutually consistent (see also Etienne et al., 1993). In Experiment 3, this was achieved by omitting disorientation of the rats' vestibular system at the start of each trial and by not rotating the polarising cues between trials. In addition, the polarising cues were absent on the unrewarded trial of each day, thereby increasing their correlation with reward. Posttraining tests explored the relative contributions of vestibular and visual cues as well as the role of landmark stability.

### Methods

*Subjects* The subjects were 12 male Lister hooded rats, selected from 18 after day 2 of training. They were treated exactly as the animals in Experiment 2.

*Apparatus* The Apparatus was identical to that in Experiment 2.

*Procedures* The training procedures were identical to those in the Single landmark condition of Experiment 2 with the following exceptions: (1) The animals were carried to the starting point without rotation of the transport box; (2) The polarising cues (curtains and noise source) always occupied the same wall of the laboratory room; they were rotated by 90° for two of the transfer tests (see below); (3) The polarising cues were absent during the non-rewarded trials; the noise was switched off and the white curtain replaced by a black one; (4) The feeder was placed 50 cm East of the single landmark (rather than South as in Experiment 2), to exclude the simple strategy of withdrawal from polarising cues North; (5) There was a series of 8 transfer tests with landmarks (numbered consecutively) beginning on day 21 (Tests 1-8), 1 transfer test without landmarks but with polarising cues (Test PO, for Polarising cues Only) and 6 intermixed days of testing without either landmarks or polarising cues which, when averaged, were considered as Test NLP (No Landmarks or Polarising cues). These 15 tests were scheduled daily (day 21-35). Tests with landmarks were always 2 days apart. The procedures for these tests were as follows:

Tests 1 and 2 were identical to the corresponding tests in Experiment 2 except that

vestibular cues were available. In Test 1 landmarks were in a familiar location, in Test 2 in a novel location not used during training. Tests 7 and 8 were duplicated these conditions at the end of the test series. The purpose of these 4 tests was to re-examine the notion of landmark stability, to test the effects of familiarity of the landmark's position, and of repeated testing.

Tests 3 to 7 were designed to investigate the effects of polarising and vestibular cues with the landmark in a familiar location. In Test 3, polarising cues were absent but vestibular cues present. In Test 4, both polarising and vestibular cues were present, but with the polarising cues rotated 90° counterclockwise relative to their orientation during training, ie. these two directional cues disagreed. In Test 5, the polarising cues were rotated 90° clockwise (relative to training) and vestibular cues were disturbed by at least 10 slow rotations of the transport box (we shall refer to this as vestibular cues "absent" and justify this description in discussion below). In Test 6, neither polarising nor vestibular cues were present. In Test 7, both polarising and vestibular cues were present and in agreement.

Test PO (day 22) was conducted with polarising cues but without landmarks. Its purpose was to explore whether polarising and background cues alone were sufficient for focused search.

Test NLP (days 24, 26, 28, 30, 32, 34) was conducted with neither polarising cues nor landmarks. It was the usual extinction trial used throughout training.

## Results

*Acquisition*

During the first 4 blocks, while the feeder was visible, there was a significant decline in latency across Blocks ($F\ 3/30 = 37.94$, $p < 0.0001$), no difference in latency between the Fixed and Varied groups ($F\ 1/10 = 1.42$, $p > 0.2$) and no Landmark Stability x Block interaction ($F\ 3/30 = 1.58$, $p > 0.2$). Landmark stability had no

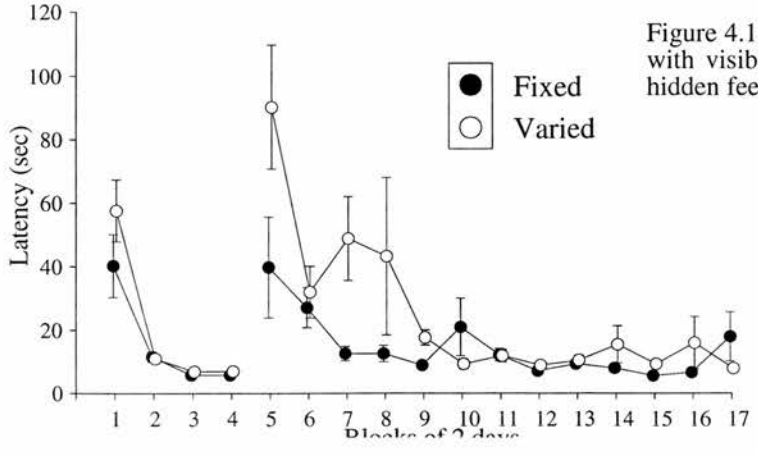



Figure 4.15. Latencies during training with visible feeder (blocks 1 - 4) and hidden feeder (blocks 5 - 17).

effect on task difficulty while the feeder was visible (Fig. 4.15).

When the feeder was hidden, from block 5 onwards, the effects of Stability ($F\ 1/10 = 12.58$, $p < 0.01$), Blocks ($F\ 12/120 = 7.14$, $p < 0.0001$) and the Stability x Blocks interaction ($12/120 = 2.32$, $p < 0.02$) were all significant. Further analysis showed that the faster latencies in group Fixed were only present on Blocks 5, 7 and 8 (p's < 0.02) and that the decline in latency across Blocks was significant only in Group Varied ($F\ 12/120 = 8.07$, $p < 0.001$) but not Group Fixed ($F\ 12/120 = 1.38$, $p > 0.1$). Group Fixed appears to have learned the spatial relationship between landmark and feeder while the feeder was visible and there was, therefore, little opportunity for further improvement when the feeder was hidden.

*Tests*

The paths taken during Tests 1 & 7 (combined) and Tests 2 & 8 are shown in Fig 4.16. These show relatively focused search at F+ in Group Fixed and a more dispersed pattern in Group Varied. Analysis of the time at F+ revealed a significant effect of Stability ($F\ 1/10 = 7.34$, $p < 0.025$; Fig 4.17A). There was no difference between early and late tests ($F < 1$) but, surprisingly, there was a decrement in search at F+ if the landmark was in a novel location ($F\ 1/10 = 9.42$, $p < 0.02$; Fig 4.17A). The distance ratio measure followed a similar trend, but the effects of Stability and Familiarity narrowly failed to reach significance ($F\ 1/10 = 4.05$, $p = 0.072$, and $F\ 1/10 = 4.19$, $p = 0.068$ respectively, all other Fs < 1; Fig 4.17B). In the analysis of directional bias, only the effect of Familiarity approached significance ($F\ 1/10 = 3.85$,

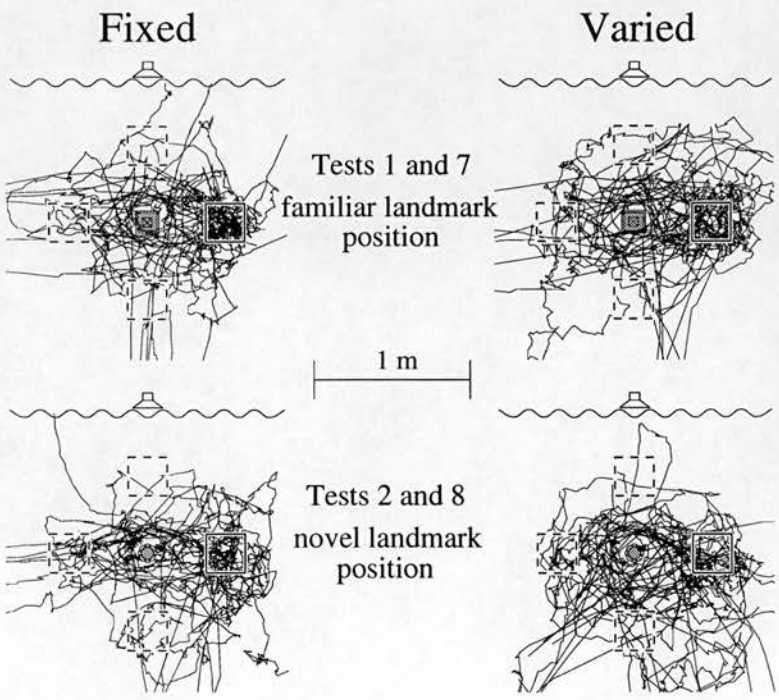



Figure 4.16. Paths during the first 30 secs of tests with familiar and novel landmark positions. Paths from early and late tests have been superimposed. Only the portion of the paths close to the landmarks is shown. The cell where F+ was placed during training is marked by a square. Other cells at equivalent distance and directions (relative to the walls of the maze) are marked by broken squares. Polarising cues (location not to scale) are situated towards the top of the page. For illustrative purposes, both landmarks are shown. They were counterbalanced within groups, but any individual rat was only trained and tested with the same landmark.

p = 0.078; all other ps > 0.2; Fig 4.17C).

The paths taken during Tests 3-7 are shown in Fig 4.18. Test 3 (polarising cues absent, vestibular cues present) shows focused search to the east of the landmark - as in Tests 1, 2, 7 and 8 of Fig 4.16. (above). In Test 4, rotation of the polarising cue by 90° counterclockwise (ie. from north to west) failed to shift the direction of maximal search from that shown in Test 3; the rats appeared, therefore, to determine the location of F+ using vestibular in preference to polarising cues. However, in Test 5, with vestibular cues absent, rotation of the polarising cues by 90° clockwise did result in the location of preferential search rotating by an equivalent amount. That is, instead of searching in predominantly the same direction as in Tests 3 and 4, the animals focused within a cell to the south (in room coordinates) of the landmark. Thus, while vestibular cues may be used in preference of explicit polarising cues, the polarising cues are sufficiently salient on their own to direct focused search appropriately. In Test 6, with both polarising and vestibular cues absent, search was no longer focused in any one direction. This indicates that the animals were not using any further uncontrolled cues. In Test 7, in which the two sets of cues were in agreement, search was focused in the correct direction to the east.

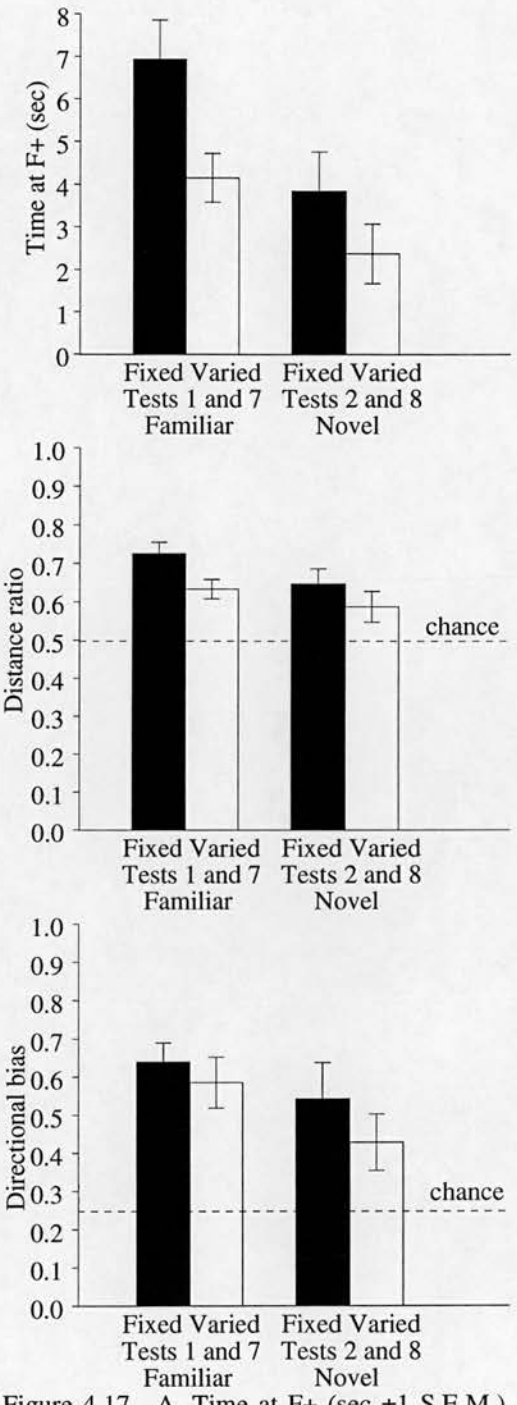


Figure 4.17. A. Time at F+ (sec ±1 S.E.M.) for Tests 1, 2, 7 and 8. B. Distance ratio. C. Directional bias.

An ANOVA of Tests 3, 5, 6 and 7 for Time at F+ revealed significant effects of Polarising cues ($F\ 1/10 = 25.65$, $p < 0.0005$) and of Vestibular cues ($F\ 1/10 = 8.98$, $p < 0.02$; Fig 4.19A). Distance ratio was higher in the presence of polarising cues ($F\ 1/10 = 6.41$, $p < 0.05$). Analysis of directional bias revealed a similar pattern to that

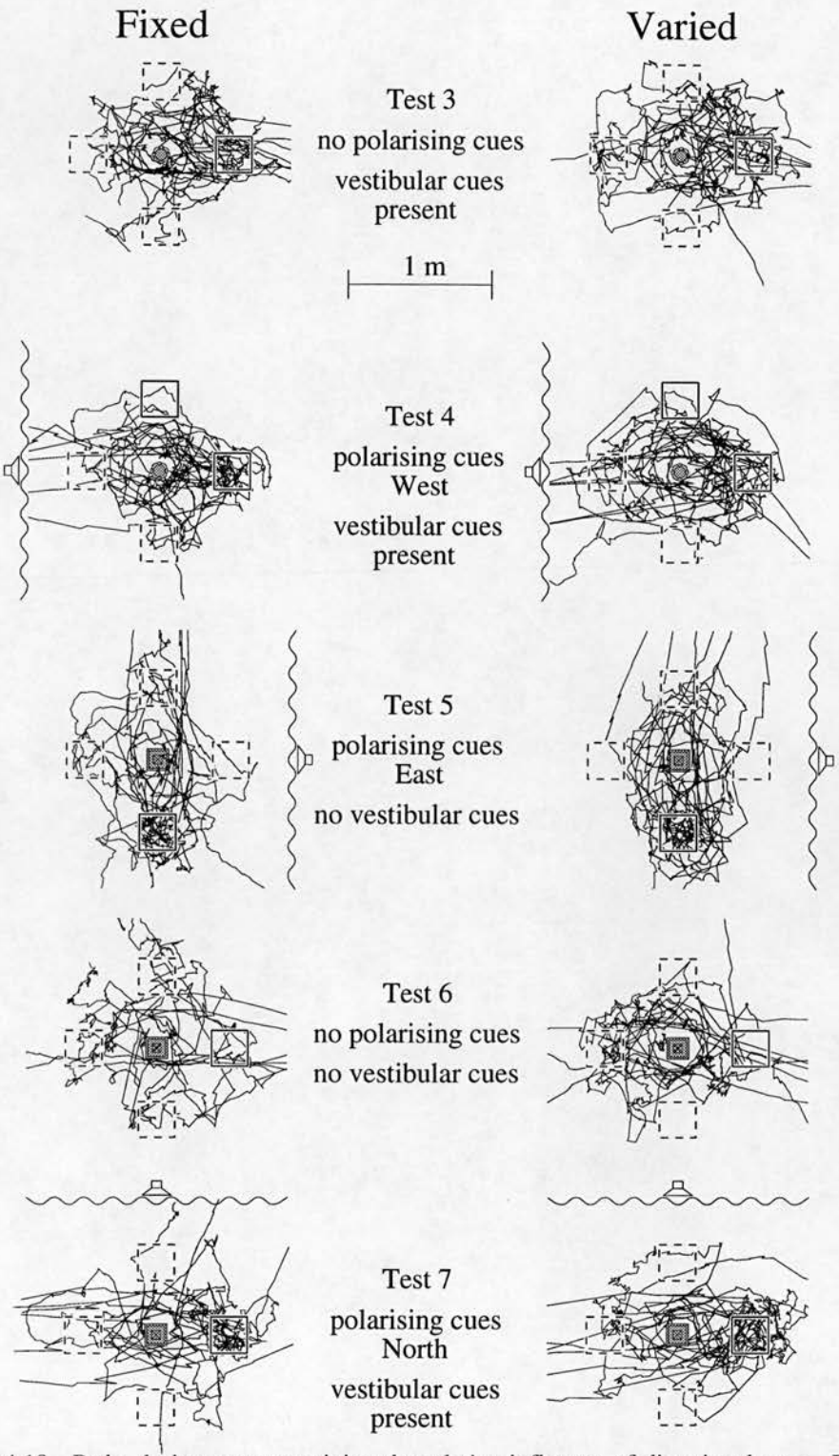



Figure 4.18. Paths during tests examining the relative influence of directional cues. Polarising cues (white curtain and loudspeaker) are shown, when present, in their actual orientation during the test (location not to scale). In Test 3, vestibular cues only were present. In Test 4, two cells are marked as F+ as the polarising cues predicted F+ to be North of the landmark, whereas vestibular cues predicted it to be in the East. The rats gave priority to vestibular cues. Test 5 shows that polarising cues could define a reference direction in the absence of vestibular cues. In Test 6, the absence of either polarising or vestibular cues resulted in the rats showing no directional preference. In Test 7, both polarising and vestibular cues were present and in agreement. Preferential search returns to the original F+ location indicating that the series of tests has not resulted in an irreversible disruption of performance. Both landmarks are shown. They were counterbalanced within groups, but any individual rat was only trained and tested with the same landmark.

shown for time at F+ : the effect of Polarising cues was reliable ($F_{1/10} = 24.18$, $p < 0.001$), while that of Vestibular cues was only marginally significant ($F_{1/10} = 3.87$, $p = 0.078$).

In the single test with polarising and vestibular cues only but no landmarks (Test PO), the mean time in the area where food had been hidden during training was no different from chance in either group (chance = 8.4 s; group Fixed = 6.7 ± 1.8 s; group Varied = 8.5 ± 1.1 s; note that the chance level varies across experiments

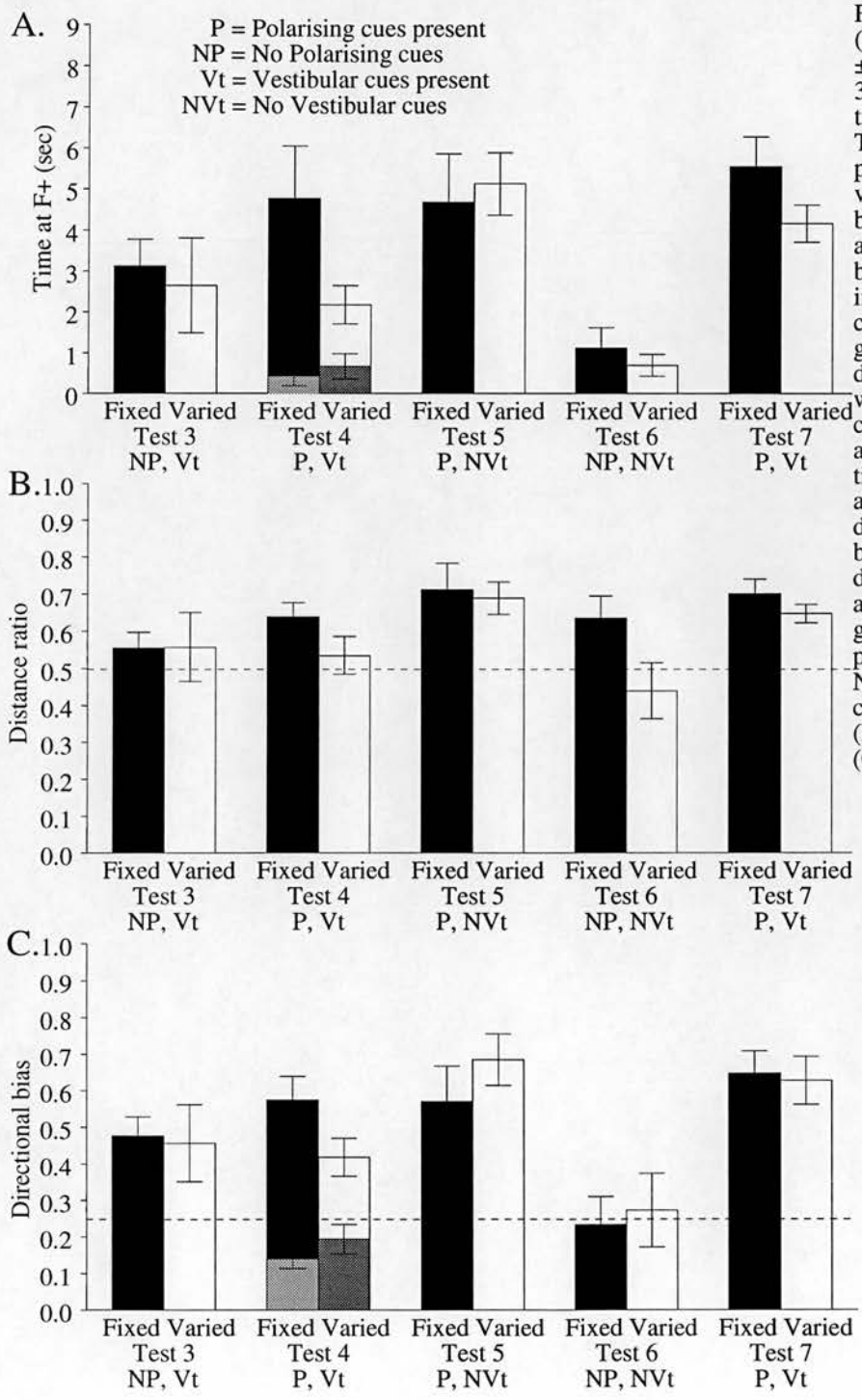



Figure 4.19 .
(A.) Time at F+ (sec ±1 S.E.M.) for Tests 3-7. The highest times are shown for Test 7 when polarising cues and vestibular cues are both present and in agreement. The black and white bars in Test 4 show data calculated using a geocentric reference direction (consistent with vestibular cues). These data are used in all statistical comparisons across tests. The dark and light grey bars show the same data calculated using a reference direction given by the polarising cues. Note that vestibular cues dominate.
(B) Distance ratio.
(C) Directional bias.

because of the variation in training protocols). In Test NLP (no landmarks or polarising cues) that time was below chance in both groups (Fixed: 2.8 ± 0.3s, Varied 3.5 ± 0.9s). Interestingly, time in the area where food could have been hidden was significantly higher in the presence of polarising cues (Test PO) than in their absence (Test NLP; $F\ 1/10 = 22.90$, $p < 0.001$).

*Comparison of Experiments 2 and 3*

Two comparisons between Experiments 2 and 3 are of interest. The first concerns the focus of this paper - Landmark Stability - examined as a function of the effectiveness of directional cues. Examining the data from Tests 1 and 2 in both experiments revealed that Time at F+ was higher in Experiment 3 ($F\ 1/22 = 13.80$, $p < 0.002$; Fig 4.20). Fixed groups spent more time at F+ than Varied groups ($F\ 1/22 = 6.48$, $p < 0.02$). The Experiment x Stability interaction was also significant ($F\ 1/22 = 5.26$, $p < 0.05$), reflecting the improvement from Experiment 2 to 3 in the Fixed condition ($F\ 1/22 = 18.05$, $p < 0.001$) but not the Varied condition ($F\ 1/22 = 1.01$, $p > 0.3$). There was also an effect of Landmark Stability with respect to Distance ratio ($F\ 1/22 = 18.05$, $p < 0.001$), but no change between Experiments on this measure. Finally, while Directional bias was stronger in Experiment 3 ($F\ 1/22 = 10.75$, $p < 0.01$), the Fixed and Varied groups did not differ overall ($F < 1$). The Experiment x Stability interaction was significant for Directional bias ($F\ 1/22 = 6.45$, $p < 0.02$), with groups Fixed ($F\ 1/22 = 16.92$, $p < 0.001$) but not groups Varied ($F < 1$) improving between experiments, as happened with the Time at F+ measure.

The second comparison examined whether the effectiveness of the polarising cues, considered in isolation, changed between experiments. The key differences were that these cues were differentially reinforced and that vestibular cues were also present in Experiment 3. We compared the average of Tests 1 and 2 in Experiment 2 with Test 5 in Experiment 3 (Fig ??). Both Time at F+ ($F\ 1/22 = 13.06$, $p < 0.002$) and Directional bias ($F\ 1/22 = 22.01$, $p < 0.0001$) were higher in Experiment 3. Thus, polarising cues were more effective in Experiment 3 than in Experiment 2 even though the simultaneously present vestibular cues took precedence when both cues were available and in disagreement.

## Discussion

The main findings of this study were: (1) landmark stability was again seen to influence spatial learning positively, although significant learning was observed in group Varied; (2) augmenting the effectiveness of the directional cues improved the accuracy of search; (3) the same polarising cues as used in Experiment 2 were found

to be effective in this experiment, although vestibular cues normally had priority; and (4) placing the landmark in a novel location not used in training was associated with lower levels of performance.

Three changes in procedure were made in this study, compared to Experiment 2, with the intention of improving the effectiveness of the directional cues. The result was that, instead of searching preferentially in four discrete locations (Fig 4.11), group Fixed now concentrated its search at one single location (Fig 4.16). While we do not know which of the three changes was the most important, we have nevertheless realised a condition in which rats, given a single radially-symmetric landmark and effective directional cues, will focus their search accurately. This finding is consistent with Collett et al's (1986) observations on gerbils, but our control of the directional cues and explicit manipulation of landmark stability have provided additional information. Performance was better in group Fixed than group Varied, with control of search by context cues alone at or below chance. This finding is consistent with our proposed principle of landmark stability.

The rats' use of directional cues has some theoretical implications. First, if the increase in the correlation between the polarising cues and reward is what has improved their effectiveness, analogous to the results of Rescorla (1968), O'Keefe and Nadel's interpretation of cognitive map theory would appear to be incorrect. Their theory makes one of two predictions in a circumstance in which a cue is only sometimes present: either the subject constructs one cognitive map of the environment but excludes this cue because it is not a stable feature - in which case the location of the food relative to the landmark could not be encoded within the map; or, two separate maps would be constructed, one with the cue and one without - and learning where the food is with the cue present should be unaffected. The theory does not predict that removing a cue from the environment on some trials could ever improve learning - the outcome that we may have obtained.

On the other hand, second, Etienne et al. (1993) have suggested that mutual correlation between visual cues and dead reckoning causes them to potentiate each other, while Knierim et al. (1995) found that creating a conflict between visual and vestibular information led rats to ignore visual cues. The latter argued that disorientation through rotation of a transport box resets vestibular cues at random. Our results are also consistent with the idea that visual and vestibular cues should be mutually consistent to be effective. There was no overshadowing of the weaker by the stronger cue. Test 4 of this experiment showed that vestibular cues have a higher

priority than polarising cues, although, in Test 5, polarising cues alone were found to be sufficient to provide a directional reference. However, when the stronger vestibular cues were made unreliable in Experiment 1, control of search direction by the polarising cues was weaker. This is consistent with the results of Jackson and Fritsche (1989) who found in taste aversion conditioning that if the salience of an overshadowing cue was weakened sufficiently, it could be potentiated. Our results do not allow us to determine definitively whether there was mutual potentiation of vestibular and visual cues. That effect would be expected from an application of a landmark stability principle to directional cues and would go beyond the results of Jackson and Fritsche (1989).

On the basis of the present data, it is impossible to decide whether increasing the contingency between polarising cues and reward, or the mutual agreement between vestibular and polarising cues, or both of these factors, were responsible for the greater effectiveness of the polarising cues in this experiment.

While I agree with Knierim et al. (1995) that vestibular disorientation can cause random resetting of rats' directional system, at least as represented by thalamic 'head-direction' cells, I believe that the resulting conflict between directional cues cannot, in this experiment, be the only factor in the devaluation of local visual cues. Test 4 of Experiment 3 established that the rats relied more on vestibular than visual and auditory polarising cues. Everything else being the same, random resetting of vestibular cues in Test 5 should have brought the group means for both Time at F+ and Directional bias to chance, while increasing variance for both measures because individual rats should have shown idiosyncratic directional preferences as strong as in Test 4. Instead, the rats disregarded vestibular information (this justifies the description of vestibular cues as functionally "absent" in tests with disorientation, rather than merely "disturbed"). I suggest that rats can reclassify vestibular information as unreliable when they are disoriented, and that this does not require previous experience (provided the disorienting rotation is above detection threshold). In other words, both the value of information and an estimate of its reliability are represented. If this interpretation is correct, it would represent a challenge to associative learning theory. A defining characteristic of associative learning is that its output is restricted to a single variable - an associative strength. Explicit representation of the reliability of a variable is not possible with existing models. Neither have models of cognitive mapping yet attempted to account for the possible representation of reliability. Obviously, a single result cannot establish this

interpretation of the data as a general feature of learning, and the question must remain open for the moment.

The performance decrement in the tests with a novel landmark location to some extent conforms to predictions of a configural or context-specificity associative account. The puzzling feature is that the Fixed group was as affected as group Varied. In the Fixed group, the novel location of L+ was only 10 cm from the two nearest familiar locations, while the nearest arena wall was 1.5 m away. However, as the search distributions of group Fixed gave no indications that localisation was accurate to within less than 10 cm when search was guided by a landmark only 50 cm away, it is puzzling that a 10 cm shift relative to walls 1.5 m away was detected. In group Varied, the novel location was 50 cm from the nearest familiar location and 95 cm from an arena wall. Accordingly, if the rats in both groups learned each training location separately, even with only 4 or 5 training trials at each location, a greater decline in search accuracy for the novel location might have been expected in group Varied, ie. a Stability x Familiarity interaction. This did not occur. The decrement in the novel landmark condition is also inconsistent with the results of Experiment 2 where only group Fixed-Clustered showed a decrement.

## 4.4. General discussion

The primary purpose of these experiments was to explore whether aspects of allocentric spatial learning can be understood in terms of established principles of associative conditioning. These include the idea that learning proceeds most readily between a stimulus and reinforcer when that stimulus is the most reliable predictor of reinforcement (Rescorla, 1968; Wagner et al., 1968). Some of the results are consistent with that principle, namely that the ability of context cues to direct appropriate searching in the absence of landmarks was greatest when they were most informative with regard to the location of the food. However, the absolute magnitude of this control was too weak to account for the effect of landmark stability, and it depended on the number of landmarks rather than their arrangement as the effect of landmark stability does. Accordingly, the results are consistent with the principle of relative validity being applicable within the spatial domain, but they suggest that varying landmark location has additional effects not predicted by associative learning theory.

In Experiment 1 the requirement for landmark stability appeared to be an all-or-nothing effect. Experiment 2 showed that local landmark stability in an array of

feeder and two separated landmarks is sufficient to support spatial learning. In Experiment 3, more effective directional cues reduced the effect of landmark stability to a quantitative difference even in a single landmark array. Nevertheless, moving landmark arrays does have some consistent effects. In contrast to the most straightforward interpretation of associative learning theory, learning about the landmark's spatial relationship to reward was impaired, not aided, by the spatial inconsistency between context cues and the landmark-feeder array. In contrast to one possible application of configural associative or context-specificity theories, landmark stability did depend on landmark arrangement. That local landmark stability can be sufficient to support spatial learning supports theories that explicitly take spatial constraints into account (Cheng, 1988, 1989; Collett et al, 1986; Gallistel 1990; O'Keefe 1991; Worden, 1992). In Experiment 2 the only difference between Clustered and Spaced landmark arrays was the number of spatial relations. In the Spaced triangular array up to nine stable spatial parameters, three distances and three angles between landmarks and feeder and three angles between landmarks, feeder and directional cues. In the Clustered array there were effectively only two stable parameters, the landmark-feeder distance and its angle to directional cues. This should only have an influence if these parameters are explicitly represented.

*Novel location tests.* In Expt 2, in group Fixed-Clustered, distance ratio decreased in the test with a novel position (Test 2). In Expt 3, time at the goal decreased in the novel position tests, while in the other two measures the decrement approached statistical significance. Had this effect occurred only or to a larger extent in the Varied condition, it would have strongly suggested that the search for food constituted a separate task for each individual landmark position. Navigation might have proceeded by matching a remembered view to the currently perceived view of the environment, with background cues and the landmark both being essential parts of this remembered view. However, it is surprising to find it in Fixed groups, where adjacent landmark positions within the grid used in training were only 10 cm apart. There is no evidence in these experiments that the rats can detect such a small displacement of the landmarks relative to walls that are 15 times as far away. Overall, the results from these tests do not fit any of the possible predictions we could think of and we must regard them as inconclusive.

*Other studies.* Studies that investigate the influence of changes of the configuration of cues on spatial behaviour may differ in several independent dimensions: (1) the maze can have an internal structure that makes choices discrete

(for example radial mazes) or search location could vary continuously; (2) the unstable cues may form a frame of reference spatially distinct from the stable cues, or they may overlap; (3) the experiment may employ a working memory or a reference memory paradigm. Not all of these combinations have been explored yet.

Kraemer et al (1983, Experiment 2) compared the acquisition rates in a working memory task in the radial maze, in which rats were trained in alternating trials with only extramaze cues or only intramaze cues available. One group received training with the intramaze cues in a consistent arrangement throughout training. For the other group the arrangement changed randomly between trials. The rearrangement was found to delay acquisition in the intramaze cue task.

Spetch and Honig (1988) trained pigeons in an open field analogue of an eight-arm radial maze. Four landmarks were placed between the eight cartons serving as food sites, and three pictures were hung on the walls. The cartons differed in colour and patterning. The pigeons in Group Constant experienced training with landmarks and pictures in consistent positions. For the animals in Group Variable the locations where landmarks and pictures were placed were the same, but they were randomly interchanged between trials. In a forced-choice test both groups were found to be above chance, but Group Constant performed better. The rearrangement of landmarks affected performance although local cues were available in the colours and patterning of the food sites.

In both these studies unstable cues did not form an internally consistent arrangement. In order to use a moving landmark array independently from other stable external cues, internal stability and spatial separation may be necessary, or at least helpful. It would create instability between two internally consistent frames of reference. In addition, it is not clear whether a choice between discrete locations makes the same computational demands as navigating to a location not marked by local cues.

Gould-Beierle and Kamil (in press) trained Clark's nutcrackers to find food near the edge of a square tray, midway between the corners and close to a landmark. When the birds were trained with the landmark in a stable position in phase 1, the peak of search followed landmark shifts parallel to the edge, but not perpendicular to the edge and only parallel component of a diagonal shift. A second phase showed that the birds relied at least partly on global cues. In an attempt to make all cues outside the tray unreliable, the tray was moved and rotated between trials. In subsequent tests the nutcrackers not only followed parallel, but also perpendicular and

diagonal shifts. This raises the intriguing possibility that the birds gave less weight than in phase 1 to the edge of the tray as a cue for distance, but still used some cue associated with the tray to determine the correct direction from the landmark. Due to the rotation of the tray during training, global cues could not provide a directional reference. Unless the birds learned each of the four orientations and tray locations separately, only the tray could give them a reference direction.

This dependence of relative weight given to a cue depending on the discrepancy to other sources of information has already been mentioned in discussion of the studies of Cheng (1988) with pigeons, Cheng et al (1987) with honey bees and Etienne et al. (1990) with hamsters (see chapter 2). The same effect has also been found in two further studies. Mackintosh (1973) investigated the recognition of territory boundaries by mice. In one experiment landmarks in a square enclosure were rotated by 35°, 60° or 90° relative to the original arrangement. The territorial boundaries followed the first two rotations. Although the 90° rotation offered a better match relative to the enclosure, mismatch to external reference increased and "*boundaries ceased to follow the movement of the objects and returned to a position substantially the same as that at the beginning of the experiment*" (p. 465). Chittka and Geiger (1995) trained bees to fly along a straight row of landmarks until they found a feeder between the third and fourth landmark. When an alternative feeder was placed at the same distance, but at a compass bearing 7.5° to the left, all bees flew to the original feeder, both under clear and overcast skies. When the row of landmarks was also shifted 7.5° left, bees started searching at the alternative feeder. This proportion of search there decreased as the landmarks were shifted to 15°, 22.5° and 30° from the original bearing. In sunny weather, offering good conditions for use of the sun compass, search at the alternative feeder was less at the smallest discrepancy and declined faster with increasing discrepancy than in cloudy weather.

Animals may classify cues according to both the accuracy and the reliability of information they can provide. In the case of visual landmarks, large and often distant features are less likely to be altered or obscured by random changes in the environment and are therefore more reliable, but only allow less accurate navigation than close small scale features. The amount of discrepancy then indicates whether the more accurate information should be trusted. The same argument applies to dead reckoning, for example in Etienne et al. Dead reckoning is prone to cumulative errors and likely has a lower angular resolution than the visual system. However, if time since the last navigational fix was short and there is a large discrepancy to a visual

cue, reliance on the visual cue would imply that the substrate over which the animal travelled has moved without it noticing, while leaving the part of the world containing the visual cue in place. In the absence of other information, it is a simpler assumption that the visual cue has been mismatched with another similar feature. It seems reasonable to assume that the same principle is at work during learning, and gives rise to the landmark stability effect.

In these examples accuracy and reliability are negatively correlated. If it could be shown that such a constraint is built into animals' navigational systems, and its appearance in such diverse taxa suggests it is a general constraint, it would be interesting to investigate the same issue in conditioning tasks. There it appears reasonable to expect that accuracy and reliability would be independent factors.

Brodbeck (1994) demonstrated a hierarchy of spatial information in black-capped chickadees, a food-storing species, but not in juncos, a non-storer. The birds were trained in a spatial delayed matching to sample task. In the sample phase they were exposed to four trial-unique feeders in a trial-unique array. Food was hidden in one of the feeders. During training the array was the same in the test phase. In experimental trials the global spatial location, the array-based spatial location and the colour and pattern of the previously baited feeder were dissociated. Chickadees showed a strong tendency to search first the feeder in the correct global location, then in the correct array location, then the correct pattern. Juncos showed no preference for any type of cue, but chose last the feeder that did not match any criterion.

If hierarchies of cues are a consequence of a general constraint, why was none found in juncos? A possible explanation is that Brodbeck's task required only discrimination of discrete places or objects, not navigation to an unmarked location. If the experiment were repeated with the food hidden at some distance from one of four landmarks, both juncos and chickadees should search in the location specified by the shape of the array when array displacement is small, and in the location defined by global cues when the displacement is large. The hierarchy appears in chickadees even in the discrimination task because, as food storers, their memory is predisposed to store places and because the discrimination task does not require the accuracy offered by nearby landmarks.

Factors other than discrepancy may also have an influence on the weight given to landmarks. While nearby local cues are sometimes preferred (Bennett 1993; Cheng 1989; Cheng et al., 1987; Collett et al., 1986; Spetch and Edwards, 1986; Spetch & Wilkie, 1994; Spetch, 1995), this is not always the case. Margules and Gallistel

(1988) found that rats who ignored cues that uniquely specified a location in a rectangular environment could use a larger frame of reference to orient themselves and distinguish otherwise ambiguous locations. The often reported preference for extramaze cues (Kraemer et al., 1983; Olton & Collison, 1979; Olton, Collison & Werz, 1977; Olton & Samuelson 1976: see O'Keefe & Nadel, 1978 and Restle, 1957 for reviews) may reflect a strategy of using large-scale features to distinguish locations marked by similar looking landmarks or landmark arrays (Brodbeck 1994; Collett & Kelber, 1988; Spetch & Wilkie, 1994). The configuration of hills or the shape of a clearing is less likely to be duplicated than the presence of a nearby bush. Any duplication that does occur is likely to be at a sufficiently large scale that dead reckoning can resolve the ambiguity. Besides the presence or absence of discrete goal locations and the relative salience of cues, an additional confounding factor is the difference between determining either distance or direction. Many studies reporting a preference for extramaze cues have been conducted in radial mazes, where the multiple goals are distinguished by direction, while studies that found greater weighting of nearby landmarks have more often used open field mazes with landmark arrays that are usually translated, but rarely rotated. Nearby cues allow more accurate determination of distance (Cheng, 1990) while distant cues are more useful for determining direction.

The results of our experiments and of those discussed above are all consistent with the proposition that spatial representations are organised in two opposing hierarchies, with proximal landmarks being treated as more accurate and distal large scale features as more reliable. When a conflict arises, the weight given to each source of information depends on the amount of discrepancy and on its a priori reliability. That this phenomenon is found in taxa as diverse as bees, bird and mammals suggests it is a general constraint on spatial learning.

## Conclusions

The results of the three experiments on landmark stability are inconsistent with the two applications of associative learning theory to navigation that have been outlined. The most straightforward associative model predicts better control by a moving landmark than by a fixed one in our conditions. This was never found. The configural interpretation predicts worse control by a moving landmark array under all circumstances, regardless of landmark arrangement. This is also inconsistent with results. However, more complex applications of associative learning to navigation may well be able to account for our data. The vector navigation models of Collett et

al. (1986) and Cheng (1988, 1989) can be interpreted as two-stage associative processes, first an association of landmark distances and directions with a place, then association of that place with reward. The model of McLaren (1995) seems to fall into the same category. McNaughton et al. (1995) have described a model of cognitive mapping and dead reckoning which postulates that landmark information is added to the map by associative processes. The interactions between processes in such two stage models have not yet been specified in sufficient detail to derive predictions regarding our experimental paradigm.

# 5. Blocking in the spatial domain

The study of blocking and overshadowing in spatial learning tests whether the acquisition of spatial representation is goal-driven and parsimonious, adding information only where necessary, or whether it is curiosity-driven, including all information that is available. A heuristic description of blocking is that subjects do not waste resources processing redundant stimuli. If an event of interest is already well predicted by other stimuli, there is no need to divert resources to stimuli giving the same information. This principle applies in standard blocking designs where the pretrained and the blocked stimulus have the same relation to the US.

| | Phase 1 | Phase 2 | Test |
|---|---|---|---|
| Exp. Group | A -> US | AB -> US | B |
| Control Group | C -> US | AB -> US | B |

Under these conditions there is less learning about stimulus B in the Experimental than in the Control group; B has been blocked by A. Unblocking, i.e. learning about the added stimulus, occurs when the predictive relationship changes, in which case the added stimulus is informative in that it signals a new relationship. Not only increases, but also decreases in US magnitudes can cause unblocking (Dickinson et al. 1976; Dickinson and Mackintosh, 1979; Mackintosh and Cotton, 1980). Temporal relations also can have an effect. A real-time model of conditioning by Sutton and Barto (1981) predicted that if the added stimulus commences earlier, but terminates at the same time as the pretrained stimulus, then it will not only acquire associative strength, the pretrained stimulus will also lose it. This was confirmed by Kehoe et al. (1987). Barnet et al. (1993) found that different timing of pretrained and added stimulus generally caused unblocking, even if the added stimulus was not the earliest predictor of the US, as required by Sutton and Barto (see also Schreurs and Westbrook, 1982). Barnet et al. conclude that organisms detect and encode temporal relationships, and that even simple associations are not so simple.

Even if accepting that a principle of parsimony applies in spatial learning, these considerations suggest two reasons why blocking might not occur. Both are consequences of the fact that navigation occurs in two or three dimensions, rather than the single dimension of either predictive relations or temporal relations. First, use of additional cues is likely to increase the accuracy of navigation. In that respect an added cue in a blocking design would not be redundant, as long as it is in a location sufficiently different from those of pretrained cues. Second, even if

pretrained cues offer enough information that added cues will not improve accuracy, in two dimensions it is possible to put an added cue in a spatial relationship that is different from that of pretrained cue and reward, but equivalent. Specifically this would mean putting an added cue at the same distance but in a different direction from reward, as there is evidence for weighting according to distance (see general discussion in chapter 4), but not according to direction. When giving pretrained and added cue different predictive or temporal relationships, these cannot be equivalent because there is only a single dimension to change. Altering temporal relations will make the added cue either an earlier, or a closer and more accurate predictor than the pretrained cue. In the two or three dimensions of space, an added cue can be at the same distance as a pretrained cue, and therefore offer the same accuracy of navigation on its own, yet it can be in a different location. This suggests that blocking might occur if a landmark is placed directly adjacent to a pretrained one, the equivalent of the Clustered condition of Experiment 2, but not if the added landmark is at some distance, in a Spaced arrangement.

There are, then, three possible predictions regarding blocking in the spatial domain. Associative learning theory doe not consider landmarks to be different from any other cues, so there should be blocking. A consideration of available information and task requirements in navigation requirements suggests that blocking should depend on the spatial relations between goal, pretrained and added landmarks. Blocking should occur when the added landmarks are very close to pretrained landmarks, so that the spatial relationships are nearly identical. When the spatial relations are different, and the added landmarks can make navigation more accurate, there should be no blocking. O'Keefe and Nadel (1978) argue that the cognitive mapping or locale system is not goal driven and that the representation is updated whenever changes in the environment are detected. Blocking should not occur within the locale system, regardless of the placement of added landmarks. It is even possible that learning about added landmarks would be faster in a Blocking than in a Control group, because the former only needs to insert these landmarks into an existing representation rather than create one from scratch.

## Experimental designs for the spatial domain

The adaptation of a blocking experiment to the spatial domain is not entirely straightforward. To specify a location unambiguously, the landmark or landmarks must provide information about distance and direction or else two distances and a way of deciding which of two intersections of two circles is the correct one. One

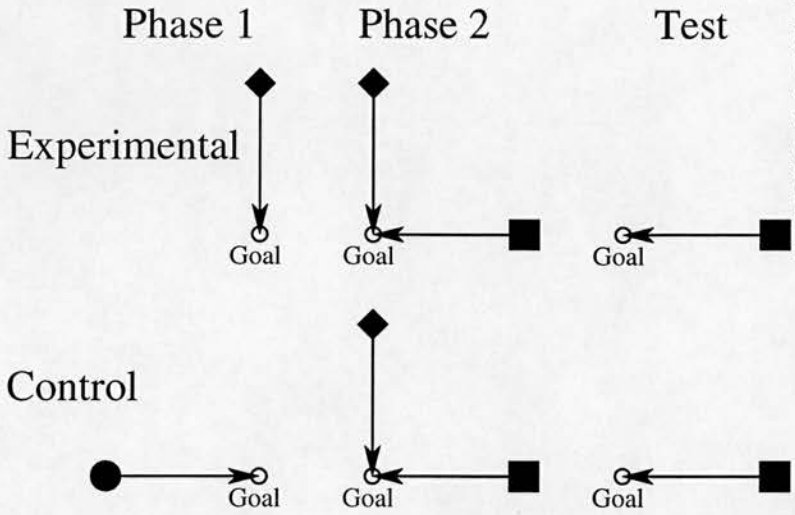



Figure 5.1. Possible experimental design for blocking in the spatial domain. Single landmarks at equal distances from the goal serve as the A, B and C cues in the standard design. Strong directional cues must be present to provide a reference direction.

possible design is the use of a directional cue and a single pretrained landmark, then adding a single second landmark (Figure 5.1). Experiments 2 and 3 showed that it is not easy to get good performance with such an array. Therefore a blocking study conducted in summer 1995 involved the use of three arrays of two landmarks each (Figure 5.2), replacing the A, B and C cues in the experimental design above. Unfortunately, for unknown reasons, performance declined drastically in all groups on transition from the compound phase, with four landmarks, to the test phase, with two landmarks. Even the Experimental group was at chance in tests with the pretrained landmarks, despite good performance in a test at the end of the pretraining phase. No analysis of blocking was possible under these circumstances, and the results are not reported.

To avoid this performance decrement, a new design was developed that minimised differences between compound training and testing. To that purpose the landmark array contained up to four landmarks of which two were present throughout all training and testing. These two landmarks were identical. On their own they could not unambiguously define reward location. Other landmarks provided that disambiguating directional information. To make sure that the rats would use primarily the identical landmarks to determine distance from food, these landmarks were closer to F+ and the rats were trained with only L3/L3 for a few days before the beginning of phase 1.

A further elaboration on the standard blocking design is that the rats were tested with both cues. In the Experimental group that means that both pretrained and novel cues are tested. In the Control group both cues are novel. This makes it possible to test whether the Experimental group reached asymptote in phase 1, by comparing

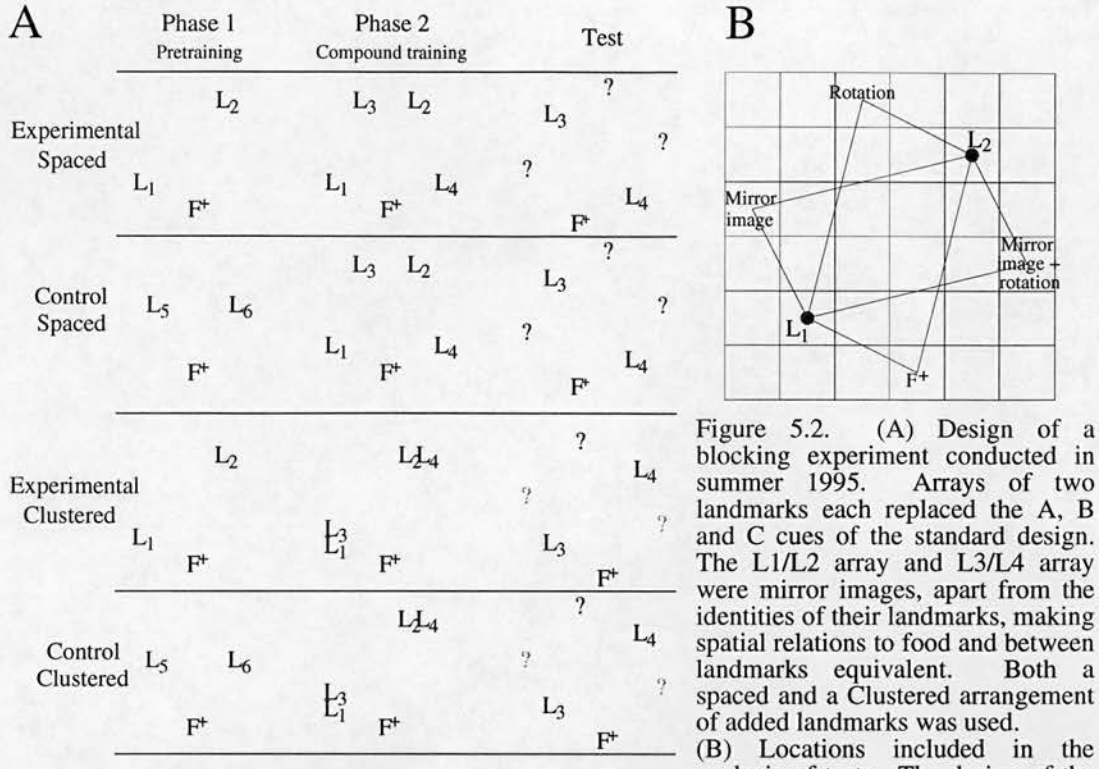



Figure 5.2. (A) Design of a blocking experiment conducted in summer 1995. Arrays of two landmarks each replaced the A, B and C cues of the standard design. The L1/L2 array and L3/L4 array were mirror images, apart from the identities of their landmarks, making spatial relations to food and between landmarks equivalent. Both a spaced and a Clustered arrangement of added landmarks was used. (B) Locations included in the analysis of tests. The design of the landmark array makes it possible to distinguish between several aspects of pretrained and added array the rats may learn. These components are: (1) distances and/or angles between landmarks and F+, (2) sense (right and left) and landmark identity, (3) discrimination of the landmarks on the basis of their proximity. If the rats have learned all three components they will search only at F+. If they know distances, angles and which landmark should be closer, but not sense (whether this landmark should be right or left) they will search equally at F+ and its mirror image. If they know only distances, angles and sense and landmark identity they will confuse F+ and its rotational equivalent. If they have learned only angles and distances they will search in all four locations. Knowledge of angles and distances is necessary for focused search. If blocking affected only some components of the task, it would show up in this design, given good enough performance of controls and of Experimentals with their pretrained cues.

performance with the pretrained landmarks in both phases, as well as pretrained landmarks with the Control group.

| | Phase 1 | Phase 2 | Test 1 | Test 2 |
|---|---|---|---|---|
| Exp. Group | A | AB | B | A |
| Exp. Group | B | AB | A | B |
| Control Group | C | AB | B | A |

In the final design (see figure 5.3 for landmark arrangements), the landmarks used as cues must not only be distinguishable by their features, they must also be placed in two different positions. That gives four combinations of landmark and position in phase 1 and the tests. To reduce variability, each test was repeated. Ignoring the two identical landmarks which are always present, the initial training with those landmarks and some counterbalancing of the test sequences, the basic design table for

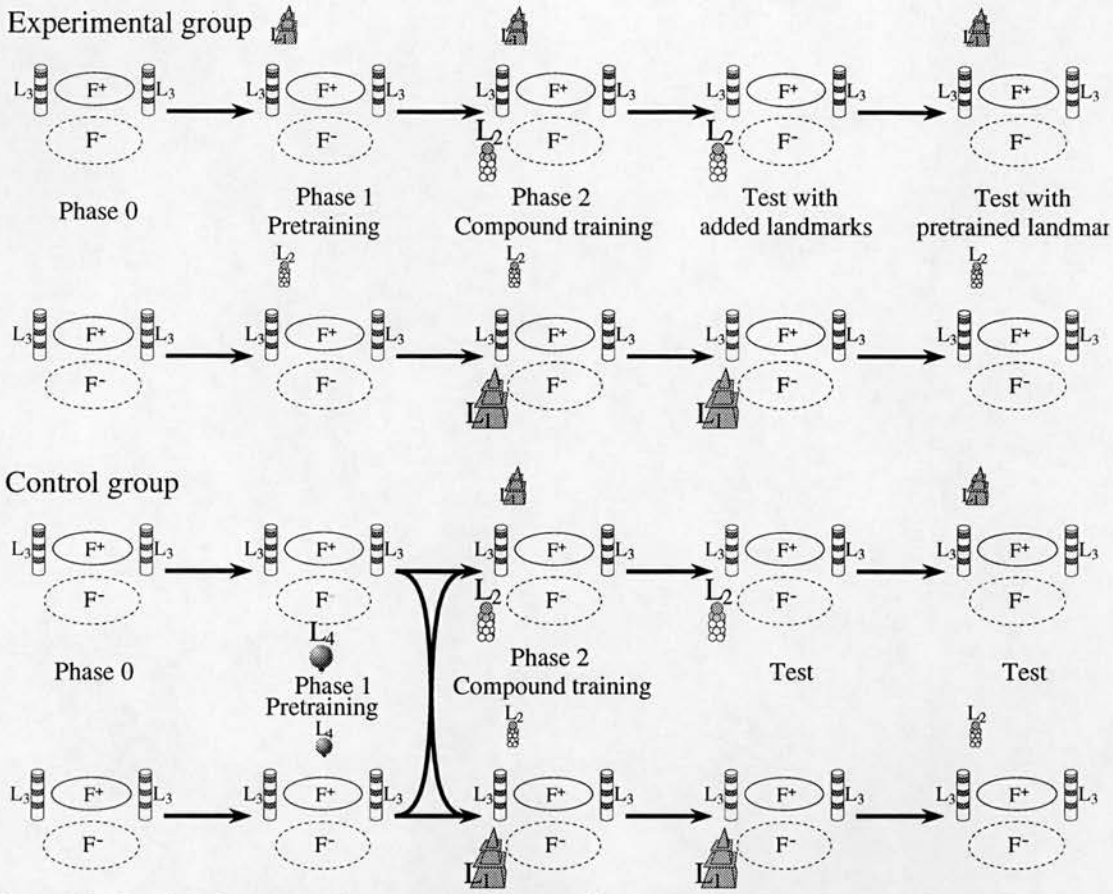



Figure 5.3. Landmark arrays and summary of the experimental design up to the second test. Rats were trained first with two identical L3 landmarks. The include radius of the F+ feeder is shown as a circle. The dashed circle opposite the L3/L3 array is the equivalent area surrounding the F- feeder. Animals' performance is measured as the preference for the F+ over the F- include radius.
For simplicity, some of the counterbalancing is not shown. Only the landmark arrays corresponding to groups Experimental 1 and 4 are presented. Each of the tests with L1 or L2 was repeated once. The sequence of landmark locations and identities in those four tests was counterbalanced.
Three more tests with all four landmarks from phase 2, with L1 and L2 changing places, and with only the two L3 landmarks, as well as two tests at the end of phase 1, are also not shown here.

blocking is as follows, where L1 and L2 are the landmarks, North and South are their positions in the array:

| | Phase 1 | Phase 2 | Test 1 | Test 2 | Test 3 | Test 4 |
|---|---|---|---|---|---|---|
| Exp. Group 1 | L1 N | L1 N/L2 S | L2 S | L1 N | L2 S | L1 N |
| Exp. Group 2 | L2 S | L1 N/L2 S | L1 N | L2 S | L1 N | L2 S |
| Control Group 1 | L4 N | L1 N/L2 S | L2 S | L1 N | L2 S | L1 N |
| Control Group 2 | L4 S | L1 N/L2 S | L1 N | L2 S | L1 N | L2 S |
| Exp. Group 3 | L1 S | L1 S/L2 N | L2 N | L1 S | L2 N | L1 S |
| Exp. Group 4 | L2 N | L1 S/L2 N | L1 S | L2 N | L1 S | L2 N |
| Control Group 3 | L4 N | L1 S/L2 N | L2 N | L1 S | L2 N | L1 S |
| Control Group 4 | L4 S | L1 S/L2 N | L1 S | L2 N | L1 S | L2 N |

# Experiment 4

## Methods

*Subjects* The subjects were 20 experimentally naive male Lister-hooded rats, maintained at 90% of their free feeding weight. 16 were selected from these after the second day of training. The rats continuing the experiment were those that reliably searched for food. 8 animals were assigned at random to each group before this selection was made. The two animals in each group with the longest latencies on days 1 and 2 were dropped, and the experiment continued with N = 8 per group. A further animal in the experimental group was dropped on day 22, and so N = 7 by the time of the first test. The excluded rat stopped searching for food when the dwell time was raised from 2 sec to 2.5 sec (see below).

*Apparatus* The arena was the same as in the previous experiments, except that there were no polarising cues. All curtains were black, and masking noise emanated from all four speakers. The reference direction was provided by landmarks. Four landmarks were used. L1 and L2 were the same as in Experiments 2 and 3. L3 was a white plastic cylinder 36.3 cm high and 7 cm diameter. There were three horizontal red stripes of 3.6 cm width. This landmark smelled of lemon. L4 consisted of a red sphere of 11.6 cm diameter above a black cylinder 5 cm high with 3.1 cm diameter, that contained cotton wool soaked in violet essence. The total height was 27 cm.

The array always included two L3 landmarks at 50 cm distance from each other. L1 and L2 landmarks were placed at 100 cm N or 50 cm S of the westernmost of the L3 landmarks. L4 could be placed 75 cm N or S of the centre of the L3/L3 subarray. The landmark arrangements in the various phases are summarised in Fig 5.3.

A new type of feeder was used that could be buried completely under the bedding and which would raise the food above the surface when triggered by a signal from the computer. It consists of an aluminium box with a sliding lid that covers a food well, connected via parallel arms to an air cylinder and damper. The air cylinder raises the box from a rectangular aluminium frame 4 cm high x 5.8 cm wide x 31.4 cm long. The total vertical movement is 5 cm. There were two feeders, F+ and F-, in the arena.

*Procedures* Pretraining: The rats had 10 days of handling and training to eat from the feeder in a separate room. This was followed by 2 days of habituation in the maze. They spent 2 half hour sessions per day in the empty arena, in groups of 4 rats.

Training: The subjects were transported to the start locations in an opaque box. They started a trial facing one of the walls in a random sequence, with the constraint that each of the 4 start positions was used once a day. They were run in groups of 7

or 8 animals, so the ITI for each particular rat depended on the latency of the others. ITI varied from about 80 min at the beginning of training to about 60 min at the end.

During the first two days of training there were 2 trials per day, both rewarded, on all other days 4 trials, 1 of them without either landmarks or reward, 3 with reward delivery in the presence of landmarks. The feeder rose automatically once the rat had spent a minimum "dwell time" within a maximum distance from the feeder ("include radius"). If these conditions were not met within 60 sec the feeder was raised automatically. A rat which failed to eat within 300 sec was picked up and placed in front of the feeder until it ate. The bedding was then thoroughly shuffled and the feeder was refilled, lowered and buried before the next rat was put in the maze. The include radius was set at 20 cm throughout the experiment. The dwell time was raised from 0 sec to 2.5 sec in steps of 0.5 sec. The feeders were placed so that the when the food well was raised it would be 25 cm from the line between the two L3 landmarks, at 35 cm distance from each L3 landmark (Fig. 5.3). Both food wells were baited to make sure potential olfactory cues were equivalent, but only one, F+, would rise while the other, F-, would remain under the surface. Which food well would rise was varied in a sequence that randomised whether the rising well or the other well was most recently baited, handled by the experimenter or touched by another rat in the preceding trial.

During Phase 0, from days 1 to 5, two identical copies of L3 were in the maze. Phase 0 training was intended to establish these landmarks as a discrete but ambiguous subarray. The two L3 landmark were present during all training and tests with landmarks. In later training phases other landmarks provided directional information that allowed an unambiguous solution. The orientation of the landmark feeder array changed in a random sequence. "North" will refer to the direction of the rising food well from the centre of the array. After day 5 the rats were matched for latency and assigned to the Experimental and Control group.

During Phase 1, from day 6 to day 28, all rats were trained with three landmarks. The Control group was split into two subgroups (N = 4) with L4 placed 75 cm either north or south from the L3 array, 79 cm from each L3. L4 north was 50 cm from F+ and 100 cm from F-, L4 south the reverse (Fig. 5.3). The Experimental group was split into four subgroups (N = 2 and N = 1 where a rat was dropped). For four rats either L1 or L2 was placed 100 cm north of the western L3, 79 cm from F+. For the other 3 rats either L1 or L2 was placed 50 cm south from the western L3, also 79 cm from F+.

The dwell time was raised by 0.5 sec on days 10, 13, 15, 17 and 19. After the last rise two rats consistently failed to find food within 60 sec. For both the dwell time was temporarily lowered. One rat did not resume searching and was dropped.

The transition to phase 2 occurred on day 28. The first two trials were with the landmark array as in phase 1, the other two trials with the full 4 landmark array. The Experimental group had one landmark added to the array of phase 1. The four subgroups collapsed into two, with either L1 north and L2 south or L2 north and L1 south. For the Control group, landmark L4 was replaced by L1 and L2. Assignment of animals trained with L4 north or south to the two arrays in phase 2 was counterbalanced. Training continued until day 49, with testing beginning on day 38.

Tests: There were two tests in phase 1, on days 24 and 27, each of 60 sec duration. As search was more focused during the first half, only the analysis of the first 30 sec reported, and all subsequent tests lasted only 30 sec. In phase 1 rats were trained and tested with the same set of landmarks.

In phase 2 there were 4 types of test. On days 38, 40, 42 and 44 rats were tested with 3 landmarks: both L3 landmarks and either L1 or L2. The sequence of testing was counterbalanced across rats. Results of these tests are reported according to landmark array, not chronological sequence. On day 46 followed a test with all 4 landmarks in their training positions. On day 48 L1 and L2 exchanged places. On day 49 animals were tested with only the two L3 landmarks, to control for possible spurious cues.

Data collection and analyses: The movements of the animals in the arena were monitored by an overhead video camera, connected to a video recorder and an Acorn A5000 microcomputer equipped with a Hawk V12 digitising board and housed in an adjacent room. Custom software recorded the time taken to find food, and the path taken by a rats as a series of x,y coordinates (Spooner et al, 1994). It was displayed, in real-time. The times spent in the F+ and F- include radii were recorded. The fraction of time at F+ out of the total time in those two circles was the preference score in tests. Because of the additional tests in phase 2, the design is not balanced. The difference between pretrained and added landmarks is a within subjects factor present only in Experimental, but not in Control groups. To deal with this unbalanced design, variances were estimated by regression and then used in t-tests to determine effects of landmark Identity (L1 vs. L2), landmark Position (north vs. south), Group (blocking) and Tests (early vs. late). This applies only to the analysis of blocking. The later tests with 4 or 2 landmarks are subjected to analysis of variance. Latencies

were not analysed, because the repeated increase of dwell time and the rising demands to search persistently would be confounded with any effect of training.

## Results

*Qualitative description*

The main findings were as follows: (1) Whether blocking occurred depended on the landmark array. Experimental animals trained with L1S/L2N showed blocking, those trained with L1N/L2S showed an enhanced preference for F+ when compared to Controls. (2) Landmarks L1 and L2 were equally effective when only one of them was present, but L1 was more salient than L2 after compound training, when the array included both. (3) Performance was better with a landmark in the North position than in the South. Navigation appears to be easier when the goal location is within the landmark array. (4) When L1 and L2 exchanged places, behaviour was not affected. The shape of the array is more important than the identity of the landmarks.

*Tests in phase 1*

The Experimental and Control group were analysed separately, because in the Control group the two possible L4 locations were not at the same distance from F+. This difference in distance would be confounded with landmark position if all data

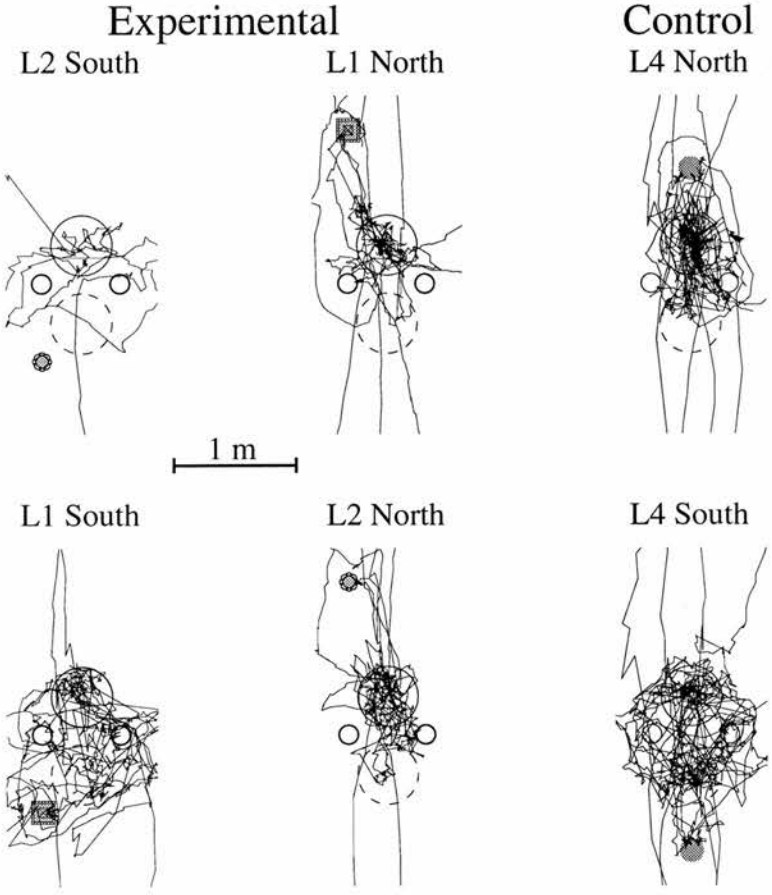



Figure 5.4. Superimposed paths from two tests at the end of phase 1. Only the part of the paths close to the landmarks is shown. Note scale bar. As in Figure 5.1, the large continuous and dashed circles are the include radii of F+ and F- respectively. Other symbols likewise correspond to a bird's eye view of the landmark arrays shown in Figure 5.1.
There are four animals in each of the control subgroups. In the Experimental groups N = 2, with the exception of the subgroups pretrained with L2 south, where one animal had to be dropped.

were analysed together.

In the Experimental group performance was good with any combination of landmark Position (North or South) and landmark Identity (L1 or L2) and in both tests (Figure 5.4). There were no significant effects of any factor (all $p > 0.2$). Rats in the Control group searched longer if trained with L4 in the North, the position closer to F+ ($F\ 1/6 = 25.3$, $p < 0.005$). This is most likely weighting according to distance. On transition to phase 2 there was extensive and selective exploration of the new landmarks, in the Experimental group either L1 or L2, in the Control group both (Figure 5.5).

*Tests in phase 2, with either landmark L1 or L2*

In the Experimental group two of the first four tests were with the pretrained landmarks, so a comparison with phase 1 was possible. First, considering phase 2 tests with pretrained landmarks on their own, there was a trend towards better performance with a landmark in the North ($F\ 1/3 = 9.77$, $p = 0.052$; Figures 5.6 and 5.7). The interaction of landmark Position and landmark Identity was significant ($F\ 1/3 = 14.28$, $p < 0.05$). This was due to search at F-, rather than F+, in tests with L2 to the South.

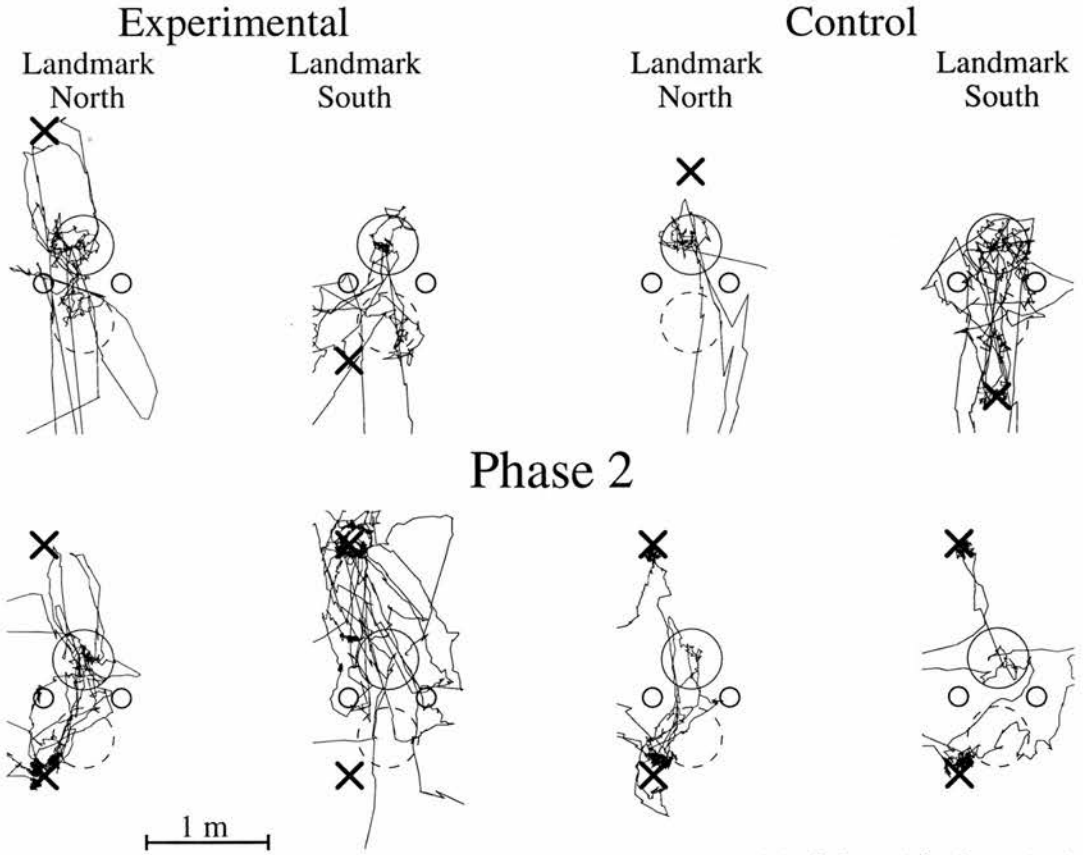



Figure 5.5. Transition from phase 1 to phase 2 on day 28. The last trial of phase 1 is shown in the upper row, the immediately follow-ing first trial of phase 2 in the lower row. In both groups the novel landmarks are selectively explored. In Experi-mentals this is only one landmark, in Controls both.

Comparing phases 1 and 2, it was found that the animal pretrained with L2 in the South shifted search from F+ in phase 1 to to F- in phase 2, when tested with the same landmark. This lead to a significant triple interaction of Position, Identity and Phase of testing ($F\ 1/3 = 18.89$, $p < 0.05$). It is inconsistent with blocking, as phase 2 training reversed the preference learned in phase 1, instead of being blocked. A replication of the experiment will show whether this is a robust effect.

Nevertheless, this and the significant preference for F- in the Control animals tested with L2 in the south ($t = 2.23$, $p < 0.05$) suggests that to examine blocking, data from animals trained with L1N/L2S may have to be analysed separately from that of animals trained with L1S/L2N in phase 2. This is confirmed by analysis of data from Controls and from Experimentals with both pretrained and novel landmarks. The effects of landmark Identity and of landmark Position are both significant ($t\ 36 = 2.34$, $p < 0.02$ and $t\ 36 = 2.99$, $p < 0.01$). The preference for F+ was stronger in tests with L1 or with a landmark in the North position (Figures 5.6, 5.7 and 5.8).

None of the double or triple interactions of Identity, Position and Group reached significance (all $p > 0.1$). Further examination of the data suggested that this lack of interactions is a consequence of mutual cancellation of different effects in tests with pretrained or added landmarks in the Experimental group, a first hint that pretraining had some sort of effect. To test this, the analyses were repeated for three separate kinds of comparison: first, in the Experimental group comparisons of pretrained and added landmarks; second, comparisons of pretrained landmarks in the Experimental group with the Control group; and third, comparisons of the added landmarks in the Experimental group with the Control group.

The general pattern is that the interaction of Identity and Position is the same in Controls as in Experimentals tested with the pretrained landmarks ($t\ 36 = 3.2$, $p < 0.002$; interaction Identity x Position x Group $t\ 36 = 0.837$, n. s.). It differs between Controls and Experimentals tested with added landmarks (Identity x Position: $t\ 36 = 0.393$, n. s.; Identity x Position x Group: $t\ 36 = 2.76$, $p < 0.01$) as well as between Experimentals tested with pretrained or novel landmarks (Identity x Position: $t\ 26 = 0.382$, n. s.; Identity x Position x Group: $t\ 36 = 3.09$, $p < 0.005$). In Control and Experimentals tested with pretrained landmarks the preference score is lowest when tested with L2 south, with other scores being similar. In Experimentals tested with novel landmarks, the score for L1 North is higher, with the other three scores similar. Put another way, when L1 South and L2 North are added landmarks, their scores are lower.

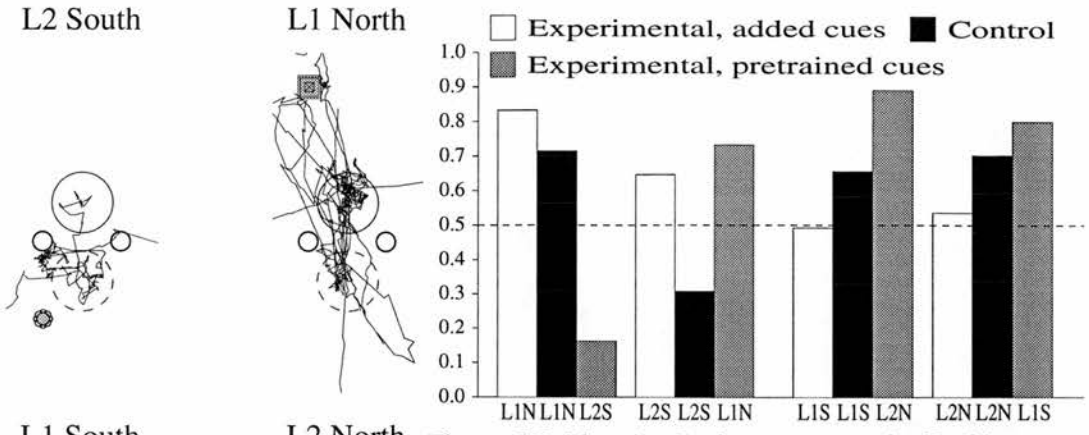



Figure 5.7 (above). Preference scores in blocking tests, which are the fractions of time spent at F+, out of the total time spent in the F+ and F- include radii. Note that the bars are ordered by array (L1N/L2S and L1S/L2N) and by rat, not by landmark within the array. A rat for which L1N was the added cue, has L2S for the pretrained cue. Experimentals trained with L1N/L2S had higher scores with the added landmarks than their respective controls, while Experimentals trained with the L1S/L2N array had lower scores, showing blocking.

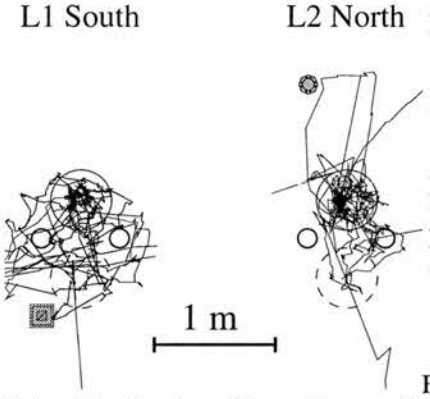



Figure 5.6 (left). Phase 2 test of Experimental animals with pretrained landmarks. The preference for F+ is as strong as in phase 1, except for the rat pretrained with L2 in the South. This animal showed a preference for F-.

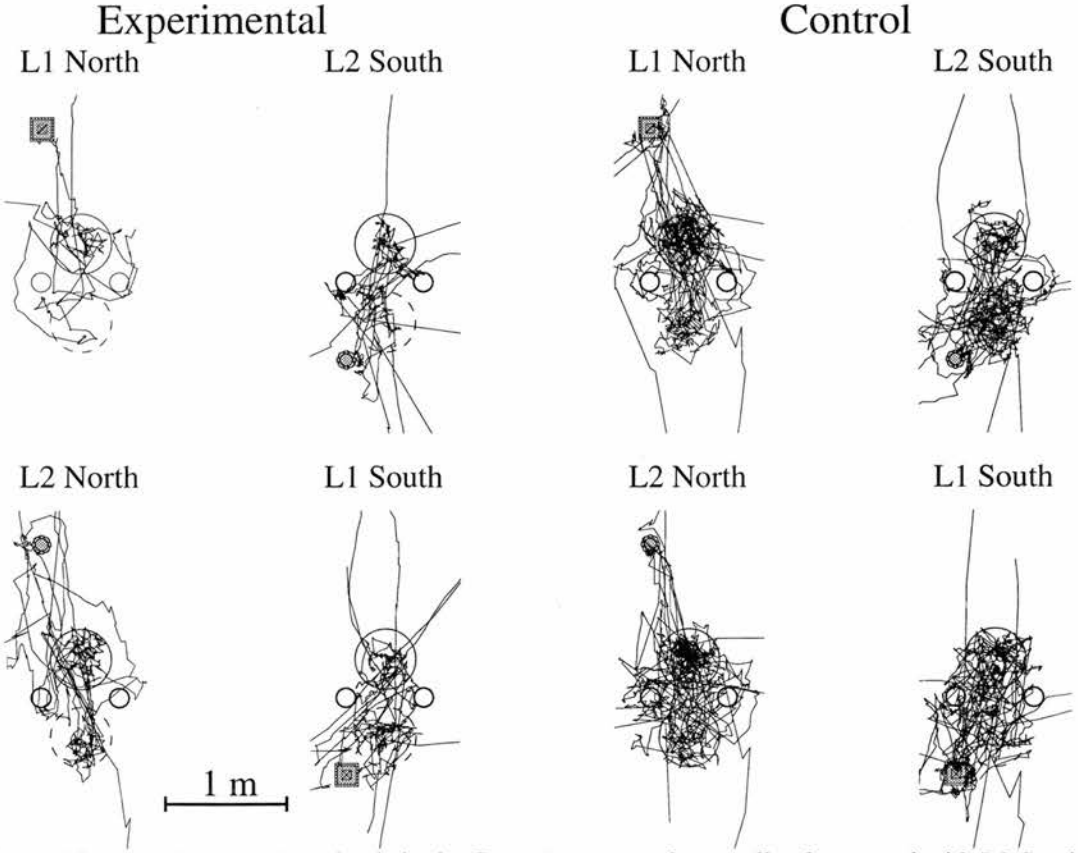



Figure 5.8. Tests in phase 2. animals in the Control group perform well unless tested with L2 South. For the Experimental group only the test with added landmarks is shown.

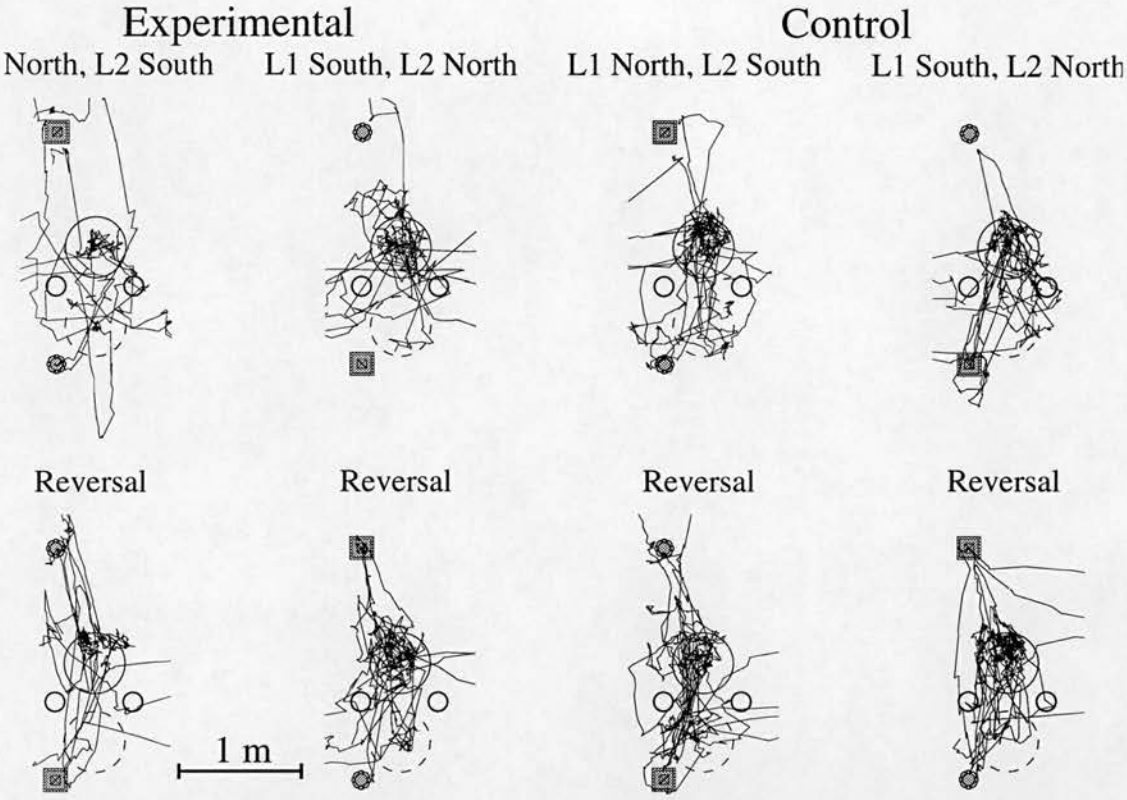



Figure 5.8. Tests with all four landmarks present, both in their original arrangement as in pahse 2 training (upper row) and with L1 and L2 reversed (lower row). The reversal made no difference to search location.

This is confirmed by comparisons between the Control group and Experimentals tested with novel landmarks. In tests with the L1N/L2S array, scores are *higher* with novel landmarks ($t_{36} = 2.112$, $p < 0.05$). In tests with the L1S/L2N array scores are lower in the Experimental than in the control group ($t_{36} = 1.77$, $p < 0.05$). There is blocking in the array in which the effects of landmark Identity and Position cancel each other and the landmarks are roughly equally salient. In the array where one landmark is far more salient because the effects of Identity and Position combine, the landmark added in phase 2

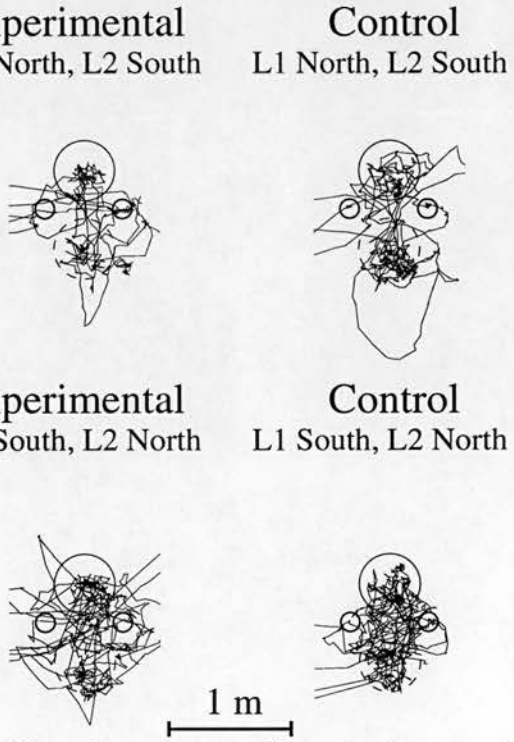



Figure 5.9. Control test with only the two L3 landmarks. Choice was at chance, ruling out control by spurious cues.

supports a higher preference score than Controls.

*Tests with 4 and 2 landmarks*

The rats were then tested with all four landmarks present, once in the same arrangement as during phase 2 training, once with the positions of L1 and L1 reversed. In these two tests both groups performed significantly above chance (all $p < 0.001$). An anova revealed a significant difference between training arrays ($F\ 1/11 = 7.00$, $p < 0.05$). Animals trained with L1 South and L2 North performed better than those with the other array. There was no other significant effect (all $p > 0.2$). Importantly, not even swapping landmarks L1 and L2 compared to their training arrangement had any effect ($F < 1$). The search location could be determined by reference to the shape of the array alone, regardless of the identity of the landmarks.

Finally, in the control test with only the two L3 landmarks animals in both groups fell to chance (both $p > 0.2$; figure 5.9). The difference between this test and the 4 landmarks tests was highly reliable ($F\ 2/22 = 28.18$, $p < 0.0001$). This shows that performance did not depend on uncontrolled cues.

## Discussion

The analysis of blocking was not straightforward due to the unexpected effects on salience of landmark identity and position. The difference in salience between L1 and L2 was surprising. In Experiments 2 and 3 the rats' behaviour did not depend on whether they were trained with L1 or L2 in a Single landmark condition. In this experiment, the difference in salience appears only if animals are trained with both landmarks. Training with either L1 or L2 (and the L3/L3 pair) in the Experimental group in phase 1 did not show any differences between the landmarks. A difference did appear in both groups after compound training, together with a landmark position effect.

The effect of landmark position cannot be weighting according to distance. The distances to all landmarks the same in the arrays with a landmark North or South. The only obvious difference is that if the landmark was North, F+ was within the array, if the landmark was South, F+ was outside the array. Although expected by Burgess et al. (1994), this is, to my knowledge, a novel finding.

If this is an important factor, it would account for another, otherwise puzzling feature of the results. Animals tested with L2 South in phase 2 were not just at chance, they preferentially searched at F-. Therefore this behaviour cannot be explained by exclusive reference to overshadowing. There must have been some erroneous generalisation. A possible explanation is as follows: If L1 is placed North,

the more salient landmark is in the more salient position. The rats may then represent only the L3/L3/L1 array, completely ignoring L2 in the South. When L1 is removed, landmark identity, the exact shape of the array, the distance of the landmark from the L3/L3 array, and the distance of L2 from the feeder do not match the learned array when the rat searches at F-. The only thing that does match is that it searches within the array, on the side of L3/L3 where there is a landmark, rather than the opposite side where there is none.

Blocking did occur when rats were trained with the L1S/L2N array, in which the effects of landmark identity and position cancelled and the landmarks were about equally salient. When landmark identity and position combined to make one landmark far more salient, performance with the added landmarks was not just equal, but higher than in the control group. It is not clear whether this is an effect of differing salience, independent of the cause of difference, or whether it is specific to spatial learning or perhaps even to this particular experimental design. Although theoretically salience does not make a difference if learning has reached asymptote (and comparisons of phases 1 and 2 show that this is the case in this experiment) in conventional blocking experiments stimuli normally have similar salience to avoid problems with overshadowing if conditioning did not reach asymptote.

The complete lack of reaction to exchanging L1 and L2 in one of the 4 landmarks tests replicates and extends the results of Cheng (1986) and Cheng and Gallistel (1984). In this situation it is the shape of the array that determines search location, not the features of the landmarks. Importantly, these are landmarks previously shown to be discriminable. In Cheng's studies the shape was defined by the walls surrounding the animal. The present study shows that shape can also have a strong influence when it has to be reconstructed from the positions of discrete landmarks. As in the work of Cheng (1984) and of Hermer and Spelke (1994), shape is only shown to be important for the determination of orientation. It has not yet been demonstrated that it is a relevant factor in determining translation.

Finally, the chance performance in the test with only two identical landmarks shows that distribution of search was controlled only by the landmarks.

Blocking in the spatial domain has so far received very little attention. Two studies had accidental similarities to a blocking design. Kraemer et al. (1983) investigated the influence and interaction of intramaze and extramaze cues in the radial maze. In phase 1 of the first experiment three groups of rats were trained with either intramaze cues alone (group I), extramaze cues alone (group E), or both (group

IE). The intramaze cues were arm inserts with different textures. In phase 2 their preference for intra- or extramaze cues was tested. With both types of cues available the animals were allowed to make three free choices and were removed from the maze. During the interval the maze was rotated through 360° in control trials, and by an angle that brought the visited intramaze cues into unvisited locations in the test trials. Choice of unvisited locations over unvisited intramaze cues indicates a preference for using extramaze cues to determine unvisited arms, and vice versa. A table shows the similarity of this design to blocking. I stands for intramaze cues and E for extramaze cues;

| | Phase 1 | Phase 2 | Test |
|---|---|---|---|
| Group I | I | IE | I vs E |
| Group E | E | IE | I vs E |
| Group IE | IE | IE | I vs E |

The two major differences are comparative testing throughout phase two and training of Group IE (the control group) with the compound in phase 1. The latter means that any difference between Group IE and the other two groups is likely to be accentuated by this additional training. Group IE reached criterion faster in phase 1 than either group I or E, with no difference between these two, suggesting no difference in salience between intra- and extramaze cues. In phase 2 group IE displayed a strong preference for extramaze cues. That effect alone could mask any possible blocking in Group E, and an analysis of blocking must rely on comparison of groups I and IE. Unfortunately, the authors make no statistical comparison between groups, though they assert that preference for extramaze cues is stronger in Group IE than in group E. Despite having been trained with intramaze cues, and although the reward rotated with the intramaze cues in the test trials, Group I initially showed no preference and then came to rely on extramaze cues. Clearly the pretraining with intramaze cues did not prevent learning about extramaze cues. In the absence of comparisons of asymptotic preference levels in these groups, or of speed of learning about extramaze cues in Group I and a group not trained in phase 1, it is not possible to decide whether learning might have been impaired or delayed.

As part of a study of navigation under minimum and redundant cue conditions Fenton et al. (1994) transferred rats in a watermaze from a two cue environment into one with either two cues added or the familiar two cues replaced by new ones. They found that rats tested with two added cues only, which they argue is similar to the experimental group in a blocking design, performed not as well as those trained only

with two novel cues. They suggested that this was best explained by reference to blocking. However, the table shows that if phase 1 is ignored this is an overshadowing design.

| | Phase 1 | Phase 2 | Test |
|---|---|---|---|
| Exptl | AB | ABEF | EF |
| Control | AB | EF | EF |

The Control group only has experience with half of the compound in the second phase. Blocking may contribute to differential performance, but this experiment cannot provide conclusive evidence.

The only two published studies explicitly designed to investigate blocking in the spatial domain were carried out by Chamizo and coworkers. Chamizo et al. (1985) studied blocking and overshadowing in the radial maze. Only three arms of the maze were used at any one time. Both groups started in a plain wooden arm and had a choice between one arm with a rubber insert and one with sandpaper. Both could see extramaze cues. In the intramaze cue condition the arms were moved between trials and reward was associated with one of the inserts. In the extramaze cue condition one of the arms always pointed in a consistent direction and reward was found in this location, regardless of the insert. In the compound condition this arm also had always the same insert. In phase 1 of the first experiment one group each was trained with intramaze and extramaze cues respectively. In phase 2 these and two control groups received compound training. Comparisons showed that pretraining with one type of cue impaired performance with the other type of cue that only became relevant in phase 2. In standard conditioning experiments the to-be-blocked cue is only introduced in phase 2. In this experiment it was present, but irrelevant, during phase 1. Therefore the impairment of the pretrained groups may be due not to blocking, but to learned irrelevance of one type of cue (N. J. Mackintosh, 1973).

To counter this objection Chamizo et al. trained two groups with intramaze cues relevant and extramaze cues irrelevant in the first phase. In the second phase both intramaze and extramaze cues were relevant for both groups. They differed in the reward contingency of the intramaze cues. In one group it remained unaltered. In the other group it reversed, the previously unrewarded cue being rewarded and vice versa. Unlike experiment 1 exposure to the conditions that could lead to learned irrelevance are equated. The authors do point out that this procedure may produce "superconditioning" (Rescorla 1971) to the newly relevant cue in phase 2. This would be expected if the unrewarded intramaze cue had become an inhibitor. The

authors argue that "a difference between the two groups in the amount learned about extra-maze cues would still indicate an interaction between intra-maze and extra-maze cues which could not be attributed to learned irrelevance" (p. 242). While this is correct, the superior learning that was found in the group with intramaze cue reversal could be attributed to superconditioning in this group instead of blocking in the other. The control procedure is not appropriate.

The inspiration for these two experiments is O'Keefe and Nadel's (1978) distinction between a taxon and a locale system, and the possibility that these systems are used in parallel (Morris, 1981). This would be analogous to the relationship between Pavlovian and operant conditioning, which establish separate associative links and therefore do not compete for associative strength. While this is a possible consequence of having separate locale and taxon systems, it is not necessary. In their discussion of "hypothesis behaviour" (p. 91 ff.) O'Keefe and Nadel rather suggest that *hypotheses* could overshadow one another. In other words, locale and taxon system compete, rather than cues within the locale system. Consequently, the specific prediction of O'Keefe and Nadel is the absence of blocking *within* the locale system, while competition between systems may lead to their overshadowing or blocking one another. In so far as Chamizo et al.'s identification of locale system with extramaze cues and taxon system with intramaze cues is correct, the first prediction was not tested, the second possibility was confirmed. Furthermore, while there is suggestive evidence that blocking between intra- and extramaze cues does exist, the procedures do not allow an unambiguous conclusion.

A recent study from the same group (Rodrigo et al., in prep.) deals with both of these problems. This study of blocking in the spatial domain was conducted in the watermaze, with discrete objects just outside the maze as landmarks, which could be removed or added at will. In an effort to keep experience the same for all animals, most trials consisted only of placing the rats on the platform. There were also some conventional swimming trials, without which rats will not search for the platform. Experimental animals were pretrained with landmarks A, B and C, then a landmark X was added. In one experiment the Controls were not pretrained with any landmarks, in another with a different set A', B' and C'. In both the Experimentals showed lower performance with landmarks A, C and X than the Controls. Experimentals also searched less in the correct quadrant with A, C and X than with A, B and C, while there was no difference between arrays in the Controls.

The balance of evidence favours the presence of blocking in spatial learning,

contradicting O'Keefe and Nadel's prediction that learning should be curiosity driven and all available information should be incorporated in the representation. The results of blocking studies are consistent with those of overshadowing. together with blocking, Chamizo et al. (1985) also investigated overshadowing between intra- and extramaze cues. Procedural ambiguities which led to the impression that extramaze cues overshadowed intramaze cues, despite taking longer to learn, were corrected by March and Chamizo (1992), who found that intramaze cues could also overshadow extramaze cues. Nevertheless, the problem remains that different types of cue are compared, with the intention of engaging different systems, although O'Keefe and

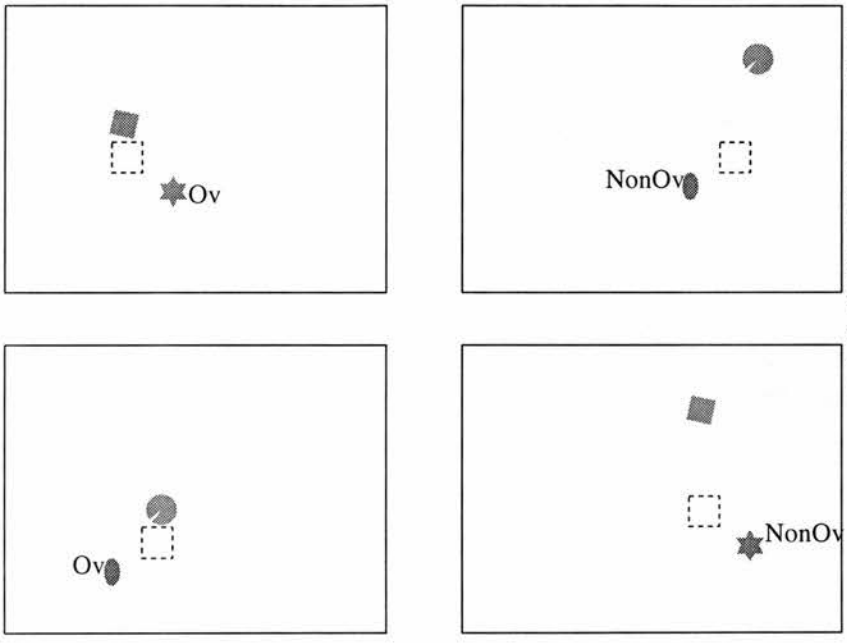



Figure 5.10. Overshadowing design counterbalanced for landmark identity and position. Subjects were split into two groups, each trained on the two arrays in a horizontal row. The goal area, shown here as a square with broken outline. was marked only early in training. Adapted from Spetch (1995).

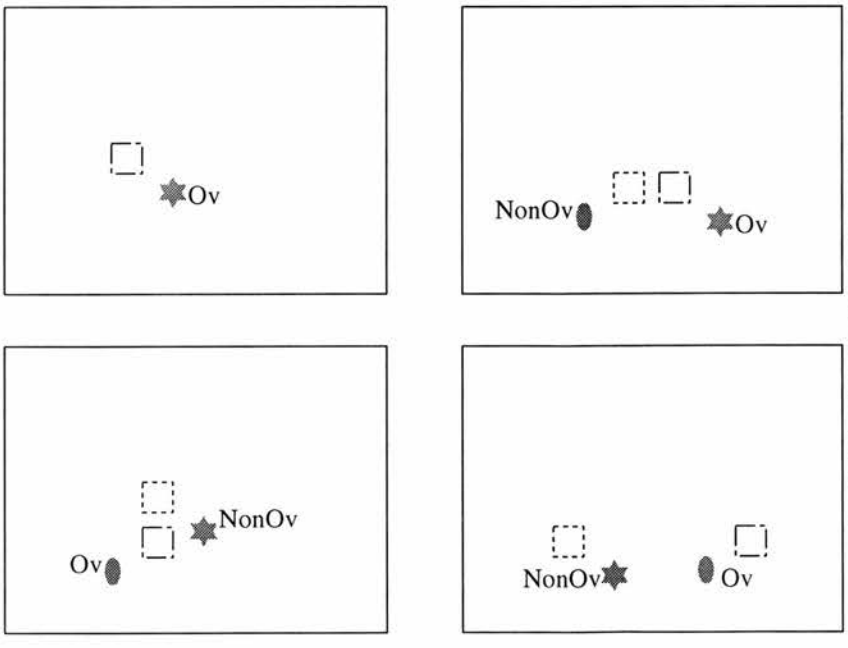



Figure 5.11. Testing procedures. Subjects were tested for their accuracy with a single landmark, either overshadowed (upper left) or non-overshadowed, or in preference tests where the landmarks from the two training arrays indicated different goal locations. This was achieved by horizontal shift (upper right), vertical shift (lower left) and swapping of landmarks (lower right). Adapted from Spetch (1995).

Nadel (1978) predict the absence of blocking and overshadowing only within one of these systems.

Spetch (1995) avoided these problems by using a counterbalanced design of cues on a touch screen. Pigeons and humans were trained to peck at or touch a small area on the screen marked only by nearby visual cues. It was expected that relative distance from the goal would determine whether a cue would be overshadowed by or would itself overshadow other cues (Figure 5.10). Tests measured both the accuracy in the presence of single cues and preference when two cues indicated different goal locations (Figure 5.11). It was found that cues closer to the goal overshadowed those farther from the goal.

It is important to note that this is different from weighting by distance. Weighting occurs after the retrieval of information. It can explain a preference for the closer landmark *within* a perceived array, and greater accuracy of navigation when using this landmark rather than a farther landmark. In this overshadowing experiment the comparison is between cues at the same distance from the goal, originally in different arrays. Therefore the inherent accuracy of navigation is the same. If, as O'Keefe and Nadel suggest, the subjects learned equally about all available cues, there is no basis for a preference or for differences in performance. The fact that accuracy and preferences did differ is evidence that different information was stored. Learning was goal driven in that it depended on what information was most useful to find a specific point. This is contrary to O'Keefe and Nadel's postulate that all information in a cognitive map is equivalent.

## Summary

O'Keefe and Nadel's characterisation of cognitive mapping included the suggestion, derived from analogy with physical maps, that information is acquired in an all-or-none fashion. There either is an entry at a particular map location or there is not. Overshadowing of one landmark by another is not possible in that case, if both landmarks are present in the map. As a criterion for the acquisition of information they suggested that the map is updated whenever a mismatch between the environment and the representation is detected. In a novel environment there is no match at all, so the animal will explore, and build up a representation. Change of a familiar environment should also create a mismatch and trigger exploration. This is independent of the amount or kind of information already stored in the map. Therefore blocking should not occur. In associative learning theory blocking is one of the phenomena showing interactions between cues. Kamin (1969) described this

as the principle that animals should only learn about those things that surprise them. If an event is already adequately signalled, there is no point learning yet another cue predicting the same thing. Only if the added cue signals a change in the relationship between events do animals learn, as shown by the phenomenon of unblocking (Dickinson et al., 1976)). In conditioning experiments overshadowing depends on the relative salience of stimuli. Animals concentrate on those cues that are easiest to notice, even if the overshadowed cue is quite adequate on its own. In both cases, learning is goal driven in the sense that learning depends on how useful a cue is to predict a particular event. Recent evidence shows that learning about landmarks is also goal-driven in this sense, rather than curiosity driven as defined by O'Keefe and Nadel. As pointed out in chapter 3, this is not a necessary feature of cognitive maps. Other definitions not including this feature are possible.

# 6. What's it all about when you get right down to it?

The two themes of this thesis are, on the one hand, the nature of navigational processes and what could be called a cognitive map, and on the other hand, what role associative learning may play in navigation. Much of the debate on whether animals navigate by cognitive maps has been dominated by O'Keefe and Nadel's (1978) definition. Even many associative learning theorists accept their arguments that cognitive mapping and associative learning are fundamentally different and incompatible processes. I have argued that possible strategies of navigation can be subdivided into more than two processes. In this scheme of classification associative learning could contribute to construction of a representation of space in most of the cases examined. I also suggest that the features of cognitive maps which O'Keefe and Nadel derived from analogy with physical maps are not an indivisible whole that would make no sense if one or several of them was left out. Furthermore, cognitive mapping is best defined as a process, an interaction between a representation and readout and planning systems. Neither representation alone nor some planning system alone is sufficient to provide the capablilities consisdered characteristic of cognitive mapping.

This final discussion will begin with the most basic question that could be asked of a navigational process, namely "how do I find X"? The properties of a process that can solve this problem suggest additional requirements one might want to add to the specification of a satisfactory navigational system. I will very briefly review the evidence for use of each of these navigational strategies.

The simplest solution to the problem of finding a place X again is to lay down a trail whan leaving X. This strategy does not even require a representation of space. As long as a trail is distinguishable from trails to other locations, it is only necessary to associate X with a specific trail. Molluscs (Blackford-Cook, 1969) and ants (Wilson, 1971) are known to lay chemical trails. This strategy has many limitations. The trail to X may be much longer than the direct path. It is not possible to determine in advance how far away X is, either in a direct line or along the trail. To get to a point Y on a different trail, a point must be found where that crosses the current trail. Predators may follow the trail (Webb and Shine, 1992). I am not aware of any evidence that there are distinguishable trails, so it may not be possible to choose between destinations on different trails at all.

These limitations suggest the following additional problems one might ask a navigational system to solve: What is an efficient path to X? What is the cost of

travelling to X? How can competitors or predators be prevented from using this information?

This last question is easiest to answer. Use information that is in memory, rather than physical markers which others can notice. What is in memory is priviledged information, until the organism communicates it. The relationship between a landmark and a destination is one kind of information that could be stored in memory. The most basic way of using landmarks is to approach a beacon, which is also one possible solution to the problem of finding an efficient path. From anywhere the beacon is noticeable and recognisable it is possible to go straight towards it, offering more efficiency than trails, and even to detour round obstacles, giving more flexibility. Sequences of beacons may be chained together. Extended cues can be followed, too. Deutsch (1960) proposed a guidance model of that kind which is adequate to account for rats' behaviour in complex mazes. This kind of model has some degree of flexibility in that it can shortcut if an animal happens to come across a stimulus further on in the chain than expected. It cannot *plan* such shortcuts, having no information about the spatial relations between beacons.

Many destinations an organism might want to reach will not be in the immediate vicinity of a landmark suitable as a beacon. In this case it may memorise a snapshot of the world as it appears from the destination. If the snapshot is only used for place recognition, navigation is possible by lining up the snapshot in a specific orientation, then moving until the next familiar place is recognised. This may be called ballistic stimulus-response chaining, as this type of landmark use only allows the organism to move until hitting the next stimulus in the sequence. This method requires either a high accuracy of response, as in its pure form there is no error correction if misses the next stimulus or else a high density of remembered stimuli. Given a high density, it is also possible to define the response in egocentric terms, as a small turn right or left (Brown and Sharp, 1995). I am not aware of any experimental evidence that would distinguish between this and a 'non-ballistic' S-R model, which would involve moving for a specific distance in a particular allocentrically defined direction. This would require dead reckoning to estimate distance. As in the ballistic S-R model, if the organism is only capable of place recognition, either the density of recognisable places must be high or responses must be very accurate. Error correction would only be possible if there is a method of approaching the centre of a snapshot, which would create a hybrid model.

Cartwright and Collett (1983) described an algorithm that uses the discrepancy between remembered and currently perceived image to compute a direction that

would take the bee closer to the goal. They found that it could account for bees' use of landmarks to approach a goal. Each snapshot has a limited catchment area in which the perceived scene is similar enough to the remembered one to allow a match. To navigate beyond that range would require chaining of snapshots in much the same way as beacons. Navigation by snapshot has the advantage of not requiring a conspicuous landmark right at the point the animal needs to reach. Like beacon navigation and the ballistic S-R method, snapshot navigation does not provide information about distances between locations. Choosing one destination among several on the basis of distance, or planning an efficient path between multiple destinations is still not possible.

If relying on landmarks alone, this type of path planning requires the capacity to perceive and store not only the angles between landmarks, but also their distances. Then it is necessary to either read the relationship between one's own location and that of the destination from a metric map, or to add self-landmark to landmark-goal vectors. A list of vectors can be used to perform all the computations supported by a map, assuming that all relevant vectors are stored in the list and that there is a procedure to detect and remove inconsistencies. Maps and vector lists are at least potentially equivalent at the adaptive and algorithmic levels of analysis. They differ primarily in implementational details. In fact, the one capacity that is necessary for all path planning based on true distances between points is vector addition, whether the vector is read from a map or computed from several individually stored vectors. When landmark arrays are distorted, gerbils (Collett et al., 1986) and pigeons (Cheng, 1988) shift their search distribution in ways that indicate use of metric relations and which are characteristically different from the behaviour of bees using a snapshot.

Landmark-based navigation necessarily uses location-specific information. The drawback is that if no familiar landmark is perceptible, the animal is completely lost. This limits how far the animal can move from familiar areas, for example during exploration. An alternative to use of landmarks is dead reckoning or path integration, the updating of position by keeping track of all displacements. This capacity has been demonstrated in many species (see section 2.5). As discussed before, dead reckoning must use metric information, so a suitable readout mechanism can recover information about distance. Bees do show evidence for the retrieval of such a stored vector when signalling the distance to a food source in a waggle dance (von Frisch, 1967). Conversely, when a bee uses information from another forager's dance, she must feed a vector into a readout mechanism. Thus at least in bees there is evidence for storage of vectors in memory and for using them as input for dead reckoning

(scheme DR3 in figure 3.1). Storage of such place codes in long term memory could occur by associations, but the updating of the current location cannot be an associative process, as discussed in section 2.5. If there are no restrictions to the combinations of place codes, this strategy of navigation already has many of the properties postulated for cognitive maps. It is possible to determine the distance and a path to a destination or distances between multiple destinations. This is the information needed to plan efficient paths between multiple goals. However, accumulating errors require that location is updated by reference to landmarks at locations other than only home.

The properties of landmark-based navigation and dead reckoning ideally complement each other. An ideal navigation system should therefore integrate the two, rather than merely using them in parallel. A quite basic form of integration occurs in navigation by non-ballistic S-R associations. Recognition of a place is the stimulus and a directed displacement over a specific distance is the response. That distance must be derived from dead reckoning. This requires a path integrator that is set to 0 when the path is first traversed, and storage of the resulting vector in memory. From there it must be retrieved and used as a target value in order to perfrom the same response again. That way only the distance between individual places would be known. Novel sequences of component paths may be created, as suggested by McNaughton et al. (1991) and demonstrated in honey bees by Collett et al. (1993). This strategy is still limited in path planning. It is not possible to determine the bee line distance between two places linked only through several different S-R associations. Only the cumulative distance along these routes is known. In a sense that makes no practical difference, as the animal would have to follow those routes anyway, having no mechanism to create a direct shortcut.

A higher degree of integration is possible if the path integrator is capable of taking any two place codes (for example the home vectors of current position and destination) and compute the difference between them (a vector between current position and destination). That would allow novel shortcutting, determination of path length and provide the information needed to plan an arbitrary route between multiple goals. Even non-metric landmark information, as from snapshots, will allow correction of random drift of the path integrator. Metric landmark information would improve accuracy, but would not be essential. Bees appear to have a representation of space that integrates dead reckoning with use of landmarks. Behavioural evidence for interactions between visual cues and dead reckoning in rodents has been reviewed by Etienne et al. (1996). They also report a recent experiment in which hamsters were shown to be capable of choosing, based on dead reckoning along a novel route, one of

four identical landmarks. More evidence for such integration comes from unit recording studies. The firing of hippocampal place cells persists in the dark, and if place fields change their locations, behaviour changes accordingly (O'Keefe and Speakman, 1987). Jung and McNaughton (1993) found that on a radial maze the whole set of place fields sometimes rotated relative to landmarks while retaining their radial distances and their spatial relationships to each other. If place fields were determined only by extramaze cues, or by unambiguous intramaze cues, this would not be possible. If place fields were driven by ambiguous intramaze cues, perhaps the shape of each individual arm, There would be no consistent relation between fields in different arms. The actual results imply that place fields can be driven by dead reckoning. In a cylindrical environment place fields could likewise rotate relative to visual cues (Knierim, 1995; see discussion in chapter 4). McNaughton et al. (1994) placed rats in a novel environment and after some time rotated it quickly. If the rotation occured very soon, the set of place fields typically retained its geocentric orientation. If the rats had more time to bind place fields to visual cues, they followed the rotation. This implies that place field firing is initially maintained primarily through dead reckoning. The unit recording studies also favour a representation in the form of a two-dimensional map over vector lists.

The questions asked of navigation up to this point, and the methods suggested to solve these problems, have only covered path planning up to the point of finding an efficient path either to a single or between multiple destinations. O'Keefe and Nadel's analogy with physical maps suggested some additional properties. One of these is instantaneous transfer. As long as landmarks are identifiable and can be used to localise a map user, it is possible to determine the relation between the map user and any location on the map, regardless of whether this person has ever been anywhere near this location before. The map is instantly usable, without prior experience of this region. A vector-sum method of navigation should provide this capacity. Two questions are important when considering the importance of instantaneous transfer for the cognitive map concept: Is transfer a necessary property of a map? If transfer exists, are there processes other than mapping that could account for it?

The first question can be answered both in general and by reference to specific examples. The general answer is that instantaneous transfer depends on the capacity to access all information in the map regardless of one's location in the represented space. However, this capacity is a property of the readout mechanism, not of the map. For a specific case, consider again the models of hippocampal function discussed in chapter 3. They all rest on the assumption that location in two dimensions is encoded

by patch of neural activity moving on a two-dimensional surface, a direct analog mapping. (That there is no topographical mapping between place field and place cell locations is functionally irrelevant; see appendix.) In Brown and Sharp's model place fields are assumed to be created by associating multiple directional local views with each place cell. This is only possible when the animal is at the location of the place-field- to-be and can perceive the local views. Therefore this type of place field map cannot possibly provide landmark information in places that have not previously been visited. The landmark arrangement visible from the novel location would simply not fit anything stored in the map. Instantaneous transfer is therefore not a property of all possible mappping systems. In the case of hippocampal place cell maps it would require a way of adding landmark information to cells whose place fields have never been visited. The analogy of the paper map, where all landmark information can be read regardless of location, is seriously misleading.

As for the second question, instantaneous transfer does not depend on use of maps. The alternative implementation of a metric place code, in terms of vectors decomposed into two components, would not suffer from any restriction on where landmark information can be accessed. The reason is that a vector list does not contain any place codes at all, except for landmark-goal vectors. Whenever an animal is not at a goal, it must perform vector addition to determine its relation to a goal. Where it is in relation to landmarks is immaterial. Therefore lack of instantaneous transfer could even be considered evidence in support of maps and against vector lists. Navigation by snapshot likewise could support instantaneous transfer, if a snapshot can be formed quickly and accurately enough. Once a snapshot is formed, it can be reached from any location within the catchment area. Instantaneous transfer can only distinguish between representations that depend on exploring an area to use landmarks there and those that do not need that much exploration. As discussed in section 3.2, that does not correspond to a distinction between cognitive mapping and associative learning.

Another set of features suggested by analogy with physical maps concerns the conditions of information acquisition. O'Keefe and Nadel predicted that variability in the spatial relations between objects should make it difficult or impossible to acquire a map. The experiments on landmark stability offer only qualified confirmation, as discussed at length in chapter 4. Learning is is influenced by the number of stable spatial relations (Experiment 2), which speaks against navigation by snapshot, but the learning under some conditions despite global instability shows that local stability is sufficient. If a map cannot deal with instability, then it must be possible to construct

rather small local maps. The predictions of mapping accounts and others then become more difficult to distinguish, as shown by the development of procedures and design from Experiments 1 to 3. The best hypothesis concerning the functional significance of landmark stability effects appears to be resistance to error. Information is classified according to two criteria, reliability and accuracy. In the case of landmarks, these are likely to be negatively correlated. As a discrepancy between two sources of information increases, the more accurate but less reliable should be given progressively less weight, as it is likely to be misleading. The results of Experiments 1 to 3 indicate that this principle applies if the discrepancy is present during learning and not only, as shown in other studies, if the discrepancy appears after learning in a stable environment.

The absence of blocking and overshadowing was another property derived from the paper map analogy. However, it is possible to use learning rules other than all-or-none incorporation of information whenever a mismatch is detected. Comparison with a hippocampal map model again proves instructive. McNaughton assumes that place cell firing is driven primarily by dead reckoning. This means the map has to be preconfigured, and therefore landmark information must be assigned to specific place cells. The learning mechanism must detect correlations, which is something associative learning does fairly well. That suggests there should be blocking and overshadowing, as has been found in several studies. Experiment 4 suggests that blocking may depend on the properties of the landmark array, but it is not clear whether this effect is specific to spatial learning, or a consequence of a large difference in salience.

The discussion of path planning has so far focused on the information provided by the representation of space. Equally important are readout and planning systems. The importance of readout mechanisms has already been shown by two examples. The models of Burgess and coworkers (1994, 1995) use essentially the same representation of space as that of Brown and Sharp (1995). The goal cells proposed by Burgess et al. can provide distance and direction to the goal, while Brown and Sharp's S-R mechanism is largely restricted to following previously taken routes, and has the capacity to cut out loops from this path but has only limited generalisation and no knowledge of distance. Bees have shown some capacity for vector addition, but appear limited in the type of vector they can retrieve at any one time. In the study reported by Menzel et al. (1996) they could only combine two inbound vectors, not an inbound and an outbund vector, which would have enabled them to make a shortcut to their destination.

Even given a rich representation and readout mechanism, there must be a way of putting this information to some use. In the case of planning an efficient path between N goals, the system must find one of the better combinations from N! possibilities. There may even be additional constraints, for example visiting rich foraging patches first, before they are depleted by competitors. Leaving aside the question how an efficient path might be computed, a powerful planning system does not necessarily imply that there is a rich representation to work with. The planning system could take its information from a metric map as well as a list of S-R responses. In the absence of vector addition its estimate of distances would be limited to the arithmetic sum of response vectors, but otherwise the problem would be the same as if information about true Euclidean distances between destinations was available. Cognitive mapping must be considered a process that includes forming a spatial representation, reading the information stored in there, and using it to plan actions. If an animal's behaviour does not meet some criterion for cognitive mapping, the cause of the limitation may lie in any or all of these domains. The creation of a map can only be the beginning of the process of cognitive mapping.

## Summary

I have attempted to analyse the properties of spatial learning not by dividing it into mapping and non-mapping strategies, but by asking what the functions are that spatial learning fulfils. I suggest that this approach allows a finer division and classification of possible navigational strategies. Most strategies in the suggested classification leave a possible role for associative learning, including the majority of what I consider cognitive mapping processes. Mapping and associative learning are not mututally exclusive; that distinction must be given up. In the absence of that dichotomy the questions of whether a particular navigational strategy is associative, becomes less important. Likewise, there is no clearcut and logical division into mapping and non-mapping stategies. The classification that follows from the questions about function and adaptive value that I have asked contains several different strategies that have the, in my opinion, most important functional properties of cognitive mapping. None has all the properties derived from comparison with physical maps. While the concept of a cognitive map still has some use, its definition by that analogy has, after many years, finally become counterproductive. The analysis also suggests that many aspects of cognitive mapping depend as much or more on the properties of readout mechanism and planning systems as on the type and organisation of the spatial representation.

# 7. Appendix

## Why is there no topographic mapping of place field to place cell locations in the hippocampus?

**Abstract**

*The mapping of place fields onto the locations of place cells on the hippocampal surface is non-topographic. It is suggested that non-topographic mapping in conjunction with use of multiple reference frames allows individual cells to code for locations in several reference frames. Storage capacity increases in direct proportion to the number of reference frames per cell, at the price of increased sensitivity to noise.*

There is no recognisable topography in the mapping of place fields to hippocampal place cells (Gothard et al., 1996; O'Keefe, 1976). Neighbouring place cells do not have neighbouring place fields, although numerous examples are known of the mapping onto anatomical space of either spatially distributed sensory input (for example retinotopic and tonotopic mapping) or computational parameters (Gallistel 1990, Knudsen et al. 1987). The barn owl's auditory system even recreates a topographic map of the direction of auditory stimuli from intensity and phase differences of sounds, stimuli that are not spatially distributed on the sensory surface (Knudsen et al. 1987). Why then is there no mapping of space to space in the hippocampus?

To address this question, assume there were topographic mapping. In this discussion I make the further assumptions that each place field has a two dimensional Gaussian shape, that place fields are equally sized (in reality the fields of place cells in the ventral hippocampus are larger than in the dorsal hippocampus; Jung et al. 1994), homogeneously distributed, and that they overlap. Place fields are larger than the possible resolution (Wilson and McNaughton 1993) and position is specified not by a single cell, but by an ensemble of active cells. If there were topographic mapping between space and hippocampus, the spatial distribution of activation in the hippocampus would replicate the distribution of active place fields in the environment (Figure 7.1). The cells of an ensemble would form a patch of activation on the hippocampal surface. The number of cells in this patch is determined only by the size and density of place fields. All and only those cells are firing that have place fields that overlap with the current location, or in other words the centres of their place fields are no more than the field radius from the current location. Furthermore, a strict one to one topographic mapping, such that neighbouring cells *always* have neighbouring fields, has two implications: First, within this patch there are no cells that are not active, If cells A and C are both firing, and there is a cell B between

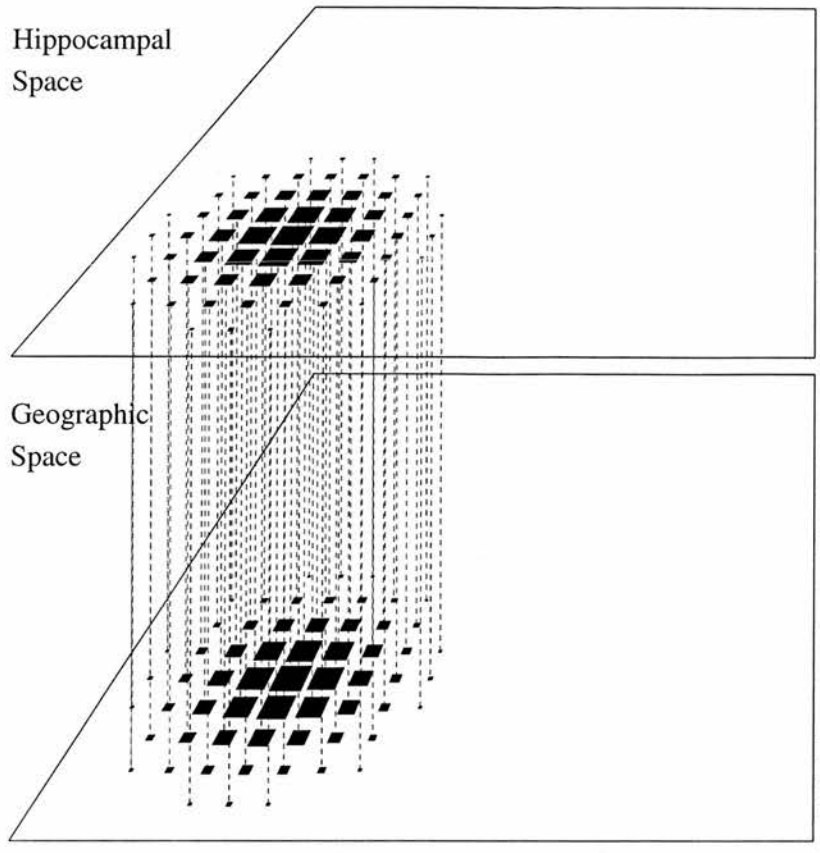



Figure 7.1. Topographic mapping of the spatial distribution of place fields in geographical space to place cells on the hippocampal surface. The animal is at the centre of the place field with the highest firing rate. In "hippocampal space" the location of each black square represents the location in the hippocampus of a place cell that is currently firing. The size of each square represents the firing rate. The same firing rates and the locations of the centres of the corresponding place fields are represented by the black squares in "geographical space. Broken lines connect each place field to its corresponding place cell, illustrating the topographic order. Each place cell is assumed to have a place field with a two dimensional Gaussian shape. The fields are assumed to have equal spread and to be homogeneously distributed. Then the firing rate of the overlapping fields necessarily reproduces the shape of individual place fields. In this example the topographic mapping is so strict that all cells, and only those cells, that have place fields centred within the place field of the central cell are active at any one time.

them, then cell B has a place field between fields A and C and therefore cell B must fire as well. Second, no cells are active outside the patch. Any cell D beyond the radius of the active cell patch also has a place field beyond the radius of the central place field.

The cells within a patch may constitute a stable cell assembly such that activation of one cell will activate the other cells of the assembly. This might be achieved through a synaptic interaction whose strength decreases as a Gaussian function of the distance between place fields (McNaughton 1996). However, the details of how the topographic mapping from place field to place cell distribution is achieved is not important for this argumant. Even the assumption of stable cell assemblies is not necessary. Only the topographical arrangement itself matters.

The fact that only the cells in a single patch can be active at any one time has two important consequences. First, even with very coarse coding these are likely to be only a very small fraction of the total number of cells in the hippocampus. Strict topographic mapping is inefficient in this case. Second, cells cannot have place fields

in different reference frames or coordinate systems (unless the hippocampal map is divided; see below). The active cell patches would be identical in each case and the encoded locations indistinguishable.

The ability to use multiple reference frames is desirable because they offer more flexibility than a single topographical map, at the expense of other potential problems such as discontinuities between frames and the representation of the relationships between frames. If a single topographic map of space on the hippocampal surface preserved metric relationships between place field locations, there would be islands of cells never used if the area they represent is inaccessible. Distortion of the map and reallocation of those cells to other areas is conceivable and does occur in other computational maps (King and Moore 1991, Merzenich et al. 1983a,b), but appears to be slow. An animal would need a long time to transform its map whenever leaving the boundaries of its current map, for example when migrating, leaving parental territory to establish its own, or after being expelled from its territory.

Multiple reference frames could be represented in a topographic map by dividing it into a corresponding number of separate areas. The spatial arrangement of these areas would not necessarily replicate the spatial relations between the geographic

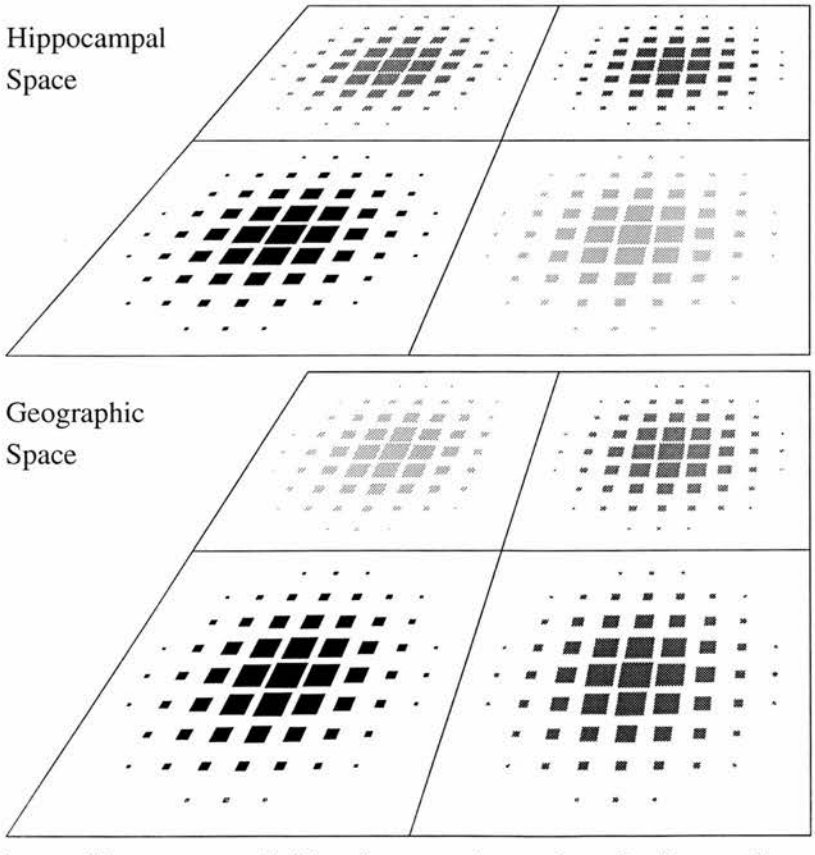



Figure 7.2. Multiple reference frames could be represented in topographic maps that are spatially separated on the hippocampal surface. The cell assemblies and their corresponding reference frames in geographic space are colour coded. The arrangement of the maps would not neccesarily reflect the spatial arrangement of the corresponding reference frames. The maps are not drawn to scale. It is assumed that the cell patches and place fields are small compared to the topographic maps and the areas they cover. Though the area allocated to each map and reference frame was kept small only for display purposes, the diagram illustrates one limiting factor to the number of reference frames. As the number grows individual reference frames become smaller. As the size approaches the spatial resolution of the map, location within a reference frame becomes less informative than location of the reference itself. There may be earlier limits due to the necessity and cost of switching between reference frames.

areas they represent. Ignoring potential boundary effects, multiple reference frames as such have no influence on the storage capacity of a strictly topographical map (Figure 7.2).

If the requirement for strictly topographical mapping is relaxed such that the diameter of a cell patch increases, the possible number of cells within a patch grows with the square of its diameter. What is the consequence of these additional cells within the range of a patch? I will assume that the number of active cells in a patch, and therefore the resolution of the map, stays constant (Figure 7.3). The remaining cells may be allocated to other reference frames. If each cell still belongs to only one reference frame, the only consequences are that the map of each reference frame has been spread out and four maps are superimposed on the same hippocampal area (Figure 7.4). Storage capacity is unaffected. Unit recording would show that only $^1/_4$ of a cell's neighbours have neighbouring place fields. There would still be recognisable topographic organisation of those cells simultaneously active at a particular time. If cell A has a place field between B and C, then its location in the hippocampus will be between B and C.

Instead of dividing the larger number of cells within the radius of the cell patch into four mutually exclusive ensembles, it is possible to create a larger number of uniquely identifiable ensembles that share some cells. Assume that each cell takes part in the representation of two randomly assigned different reference frames

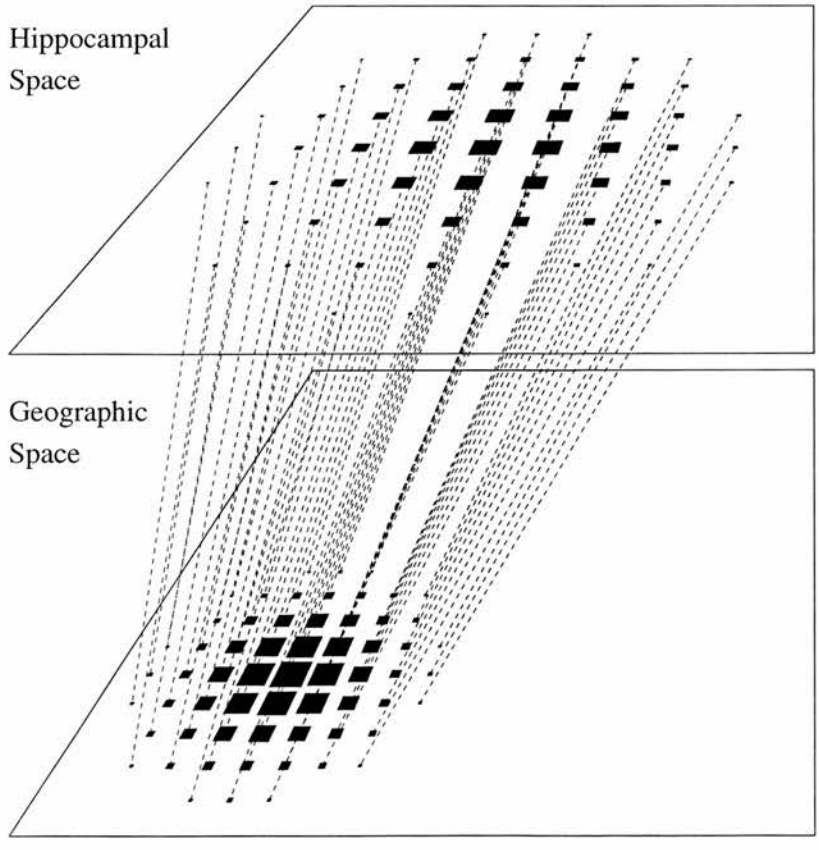



Figure 7.3. The radius $\sigma$ of the active cell patch has been doubled. If the number of active cell is constant, only $^1/_4$ of the cells within the radius of the patch are actually active. The broken lines illustrate the looser topographic mapping from place field locations to place cell locations.

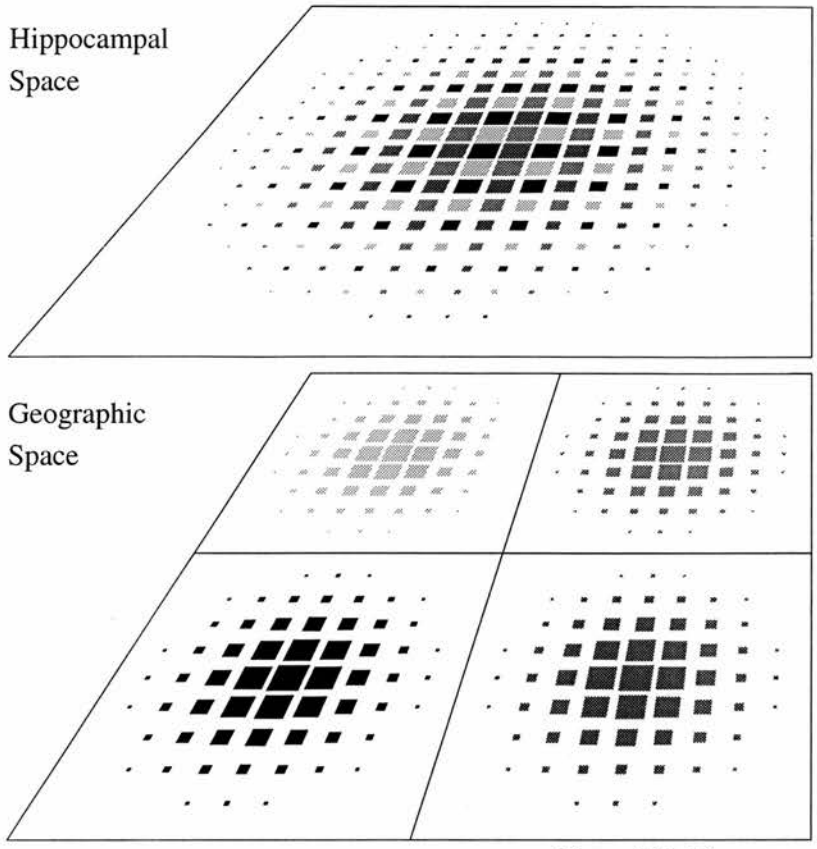



Figure 7.4. The additional cells within the radius of potentialy active cells could be assigned to four mutually exclusive cell ensembles. Then storage capacity, processing and noise sensitivity are unaffected. However, unit recording would show that only $^1/_4$ of the neighbours of any one cell would have neighbouring place fields.

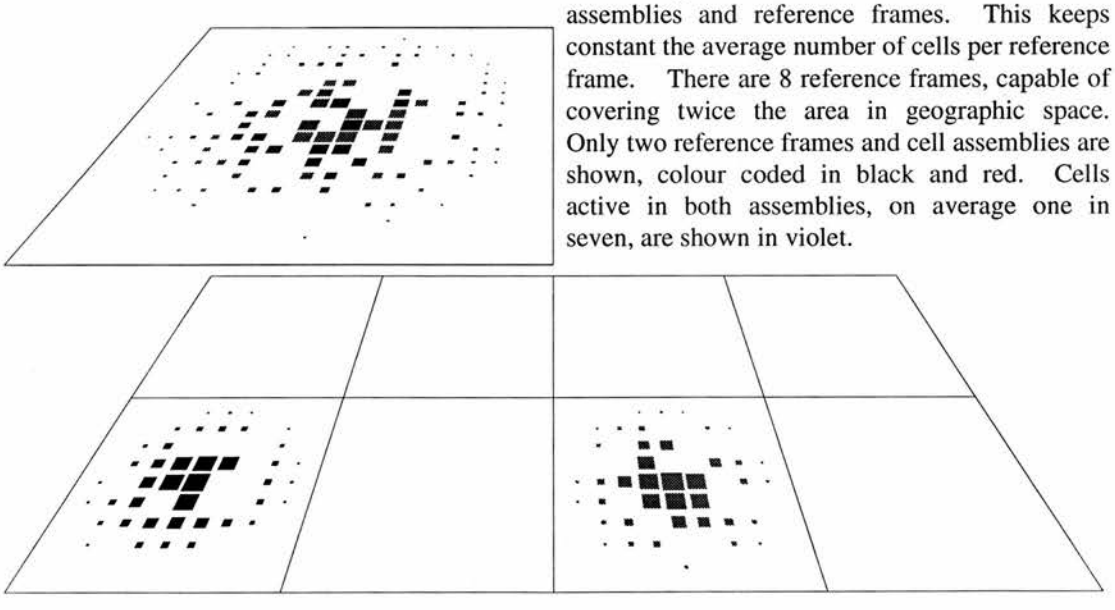


Figure 7.5. The range of synaptic interactions has been doubled relative to Figure 1. Each cell has been assigned at random to two different cell assemblies and reference frames. This keeps constant the average number of cells per reference frame. There are 8 reference frames, capable of covering twice the area in geographic space. Only two reference frames and cell assemblies are shown, colour coded in black and red. Cells active in both assemblies, on average one in seven, are shown in violet.

(keeping constant the resolution, the number of place fields per area in each reference frame). Then the same area of hippocampus contains not four but eight reference frames (Figure 7.5). Under the given assumptions, the area that could be represented in the map is proportional to the number of reference frames per cell. However, the sensitivity to noise increases. If only one cell is activated it is impossible to tell which

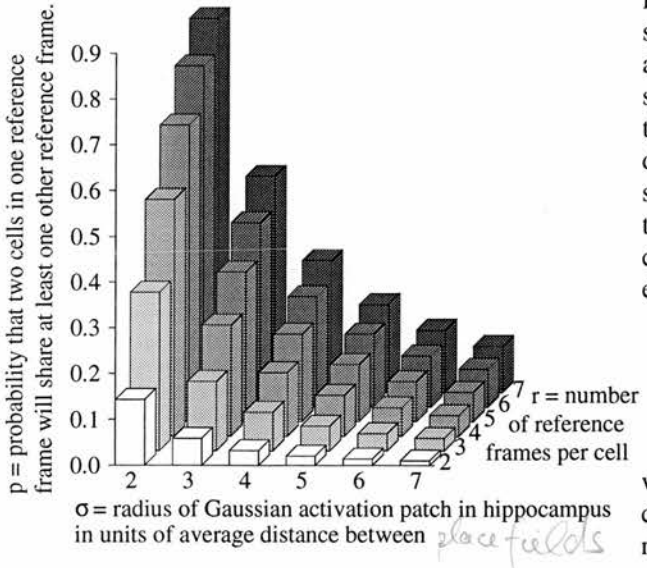



Fig 7.6. The probability that two cells sharing one reference frame will also share a second, so failing to unambiguously specify the current frame, increases with the number of frames per cell and decreases with increasing spread of synaptic interaction. Under the assumption that all reference frames for an individual cell will be different, it is given by the equation:

$$p = \sum_{i=2}^{r} \frac{\binom{n-i}{r-2}}{\binom{n-1}{r-1}}$$

where r = number of reference frames per cell and $n = \sigma^2 r$, the total number of reference frames.

of its reference frames should be active. At least two cells are needed to unambiguously specify a reference frame. As shown in Figure 7.6, the probability that any two cells will fail to uniquely identify a single reference frame, i.e. the sensitivity to noise, increases as a function of the number of reference frames per cell, and decreases as a function of the radius of the cell patch, until the limiting case when the cells of each reference frame are spread over all of the hippocampus. Distributed mapping is actually found in the hippocampus (Gothardet al., 1996; O'Keefe, 1976). Whether the mapping is actually random is not clear. If reference frames only ever represented separate areas, it would not be difficult to search for topographical ordering of the cells firing at a particular moment. However, as it has been found that reference frames spatially overlap (Gothard et al, 1996, McNaughton et al, 1995), being bound to different landmark groups, several reference frames may be in use simultaneously. Separating them by manipulation of the environment while recording a sufficient number of cells at a high enough sampling rate is extremely difficult. The possibility of loose topographic ordering of place cells within individual reference frames cannot yet be excluded.

To summarise, multiple reference frames allow not only increased flexibility, but storage capacity is directly proportional to the number of reference frames per cell. For a given noise sensitivity that number is the higher the looser the topography of a computational map is. The limiting case, found in the hippocampus, is the absence of any recognisable topography. For illustrative purposes I have assumed that multiple reference frames would cover different areas. In practice, reference frames are found within the same environment (Gothard et al, 1996, McNaughton et al, 1995), bound to different sets of landmarks. I have also assumed that they represent only spatial

relations. I cannot exclude the possibility that some reference frames may encode non-spatial aspects of the environment, while others have purely spatial content.

The reference frames discussed here are equivalent to Worden's (1992) fragments. Worden (unpublished manuscript) argues that the principle of "fragment fitting" can be applied not only to navigation, but to cognition in general. In this case storage or processing capacity would generally be greater in the absence of the mapping of computational parameters onto space.

The argument does not specifically depend on a fragment fitting model of cognition. As cognition becomes more abstract, the space of possible features becomes larger while the proportion of features present at any one time becomes smaller. For example, the feature space of an auditory coincidence neuron is limited to frequency and a relatively small range of interaural delays. Sounds containing many frequencies and originating from many directions may need to be processed simultaneously. The feature space of a visual edge detector is limited to edge orientation and retinal location. Many edges may occur simultaneously in many locations and need to be processed in parallel. In navigation, there are more possible combinations of location and orientation, only one of which occurs at any one time. Likewise, a hypothetical "grandmother cell" would need to be sensitive to a selection of features out of a very large space of possible features, at least some of them context dependent. Dedicating a single cell or group of cells to just this specific combination of features would be inefficient. Therefore topographic computational maps are most suited to parallel processing of a large amount, but limited range, of data. The use of multiple reference frames and sequential processing is preferable where the possible range of data is large compared to the amount of data processed.

The argument so far is a derivation specific to reference frames of a more general property. Topographic mapping restricts the population of cells that can be used to code for a place or other parameter. The number of different codes is equal to the total number N of units (neglecting border effects in coarse coding), while an unrestricted code would have $2^N$ different combinations, but no resistance to noise. Any random change of the state of one unit would create a different, but still valid code. In sparse coding only a small proportion of the total number of units is ever on, but they are drawn randomly from the total population. This leads to lower storage capacity, but higher resistance to noise. Is there any difference between sparse coding and use of multiple reference frames? There can be, given an additional assumption. If coding is preconfigured in the way suggested by McNaughton et al., with connections between cells based on the distances between their place fields, then each

cell can have only one place field within each reference frame. Multiple place fields within the same environment would have to be fields in different frames. The probability of a cell having two place fields close together should be lower than of the fields being distant or of finding a field for the same cell in a different environment. The probability would be zero within the radius of a reference frame only if frames never overlap.

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